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INHERITANCE AND EVOLUTION (Methuen)

TEXT-BOOK OF ZOOLOGY

By

W. F. WHEELER, M.A.
Biology Master, King Edward VII School, Sheffield

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PREFACE

A STUDENT embarking upon a course of zoology is about to discover, through theory and practice, the essential attributes of the animal organism. In order to achieve the desired results, the study of the subject must be considered from various aspects. I have attempted to provide the material for almost all of these in the following pages, and to produce a course in keeping with the more modern method of treatment of the subject. This treatment involves, in the first place, the selection of a number of types which should be studied intensively in respect both of their anatomy and physiology. Any phenomenon of especial biological significance, such as the cellular structure of animals, may be discussed *en passant* as it arises. Accordingly, the first part of this book is devoted to types selected in accordance with the general requirements of Higher School Certificate Examining Boards. The types have been arranged as far as possible in order of their evolutionary descent, though it is not intended to suggest that they should necessarily be studied in this sequence. For example, it is assumed that the study of vertebrates will begin with *Rana*. I consider this to be the best starting-point, not only on account of its comparatively simple structure, but also (and this is more important) because of the excellent opportunities it affords for practical work. With this consideration in mind, I have included sections on histology and gametogenesis in the chapter on *Rana*. With amendments in matters of detail only, the descriptions therein contained are applicable to other vertebrate types.

There follows a short account of the embryology of *Amphioxus*, *Rana* and *Gallus*. The structure of individual organs may be followed from a study of adult types, but only by ascertaining the way in which these organs come into being can the relationships between them be fully appreciated. In this connexion the importance of *Amphioxus* cannot be over-emphasised, for it displays in most respects the essentials of Chordate embryology in a primitive condition. A knowledge of this process in *Amphioxus* should certainly be acquired before the development of other types is considered.

But the student should realise that a knowledge of types is but a means to an end, and not an end in itself. When he is acquainted with the form, function and development of individual organisms, he has but accumulated the material for the construction of an edifice of real zoological knowledge. In accordance with true scientific principles he must proceed to apply this particular knowledge to the formulation of general conclusions. It is especially at this point that this book should be especially valuable, for an attempt is now made to correlate the facts so far ascertained. From the point of view of anatomy this comparative treatment has been confined to the various classes of the Chordata, for here the evolutionary relationships are easily traced. Accordingly, each system is considered in turn, and the connexion between organs in different classes is established. This is intended to give an indication of the types of change which have occurred and which bring about the evolution of one group from another.

There follows a section dealing with comparative physiology, and in this the Invertebrata have been included with the Vertebrata. An attempt has been made to elucidate the essentials of each process, and a certain amount of elementary biochemistry has been introduced. In this connexion I have to acknowledge the great help which I have received from Dr. W. R. Fearon's excellent book, " An Introduction to Biochemistry."

Throughout its life-time the animal organism is subject to its environment, both internal and external. Of the factors contributing to the internal environment of members of the various classes of the Craniata, the ductless glands are of primary importance. The chapter devoted to them is followed by one in which the relationship of the animal to its external environment, both animate and inanimate, is considered. Finally, the classification of the animal kingdom is discussed.

In respect of practical work, suggestions have been made which include notes on staining techniques and the preparation of sections of animal tissues, since these operations are not fully described in most practical text-books, all of which provide detailed instructions for dissection.

In stating my reasons for the adoption of the general plan of this book, I should like to account for certain omissions. The most apparent will be the absence of special sections on ecology and genetics, but a " potted " ecology is not only valueless but dangerous ; the student is recommended to read that stimulating book, Charles Elton's " Animal Ecology," where he will find a fund of information. Practical work in this branch of zoology is something of a local problem. For similar reasons only cursory references have been made to problems of genetics, whilst so far as possible the theme of the book is one of evolution, without treating this phenomenon as a separate entity. My chief hope is that this book may be of service to the student in the formulation of his conception of the animal organism, diverse in form and function, yet always displaying those manifestations characteristic of animal life.

A number of figures have been reproduced from various printed sources, a separate list of which is appended. I wish to express my sincere thanks for permission granted by the persons concerned. In conclusion my grateful thanks are due to my wife, who has prepared all the original drawings for publication and has rendered invaluable assistance in the compilation of the index, and to my publishers for the great care taken in production and the patient solution of my many problems.

W. F. W.

SHEFFIELD,
April, 1938.

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TEXT-BOOK OF ZOOLOGY

CHAPTER I

AMŒBA AND EUGLENA

(1) AMŒBA

Amœba belongs to the group of animals known as the Protozoa. Members of this phylum differ from all other animals (Metazoa) in that they are non-cellular, i.e. their bodies are not divided up into a number of cells.

Structure. *Amœba* itself is a minute organism, of jelly-like consistency, its entire body being composed of **protoplasm** (living matter). This is clearly differentiated into a comparatively clear **ectoplasm** at the surface, surrounding a much more granular **endoplasm.** In this latter are contained several structures of importance.

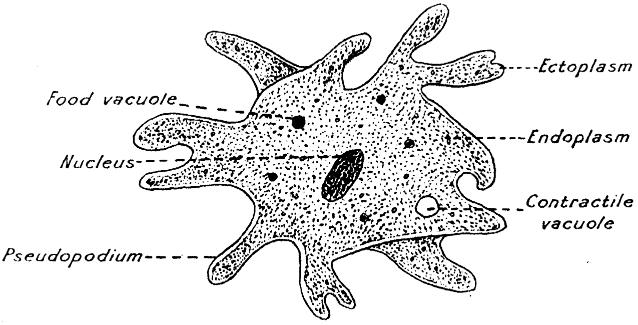


FIG. 1.—*Amœba proteus.*

The **nucleus** may be distinguished as an oval body, slightly more opaque than the remainder of the endoplasm. Its function is to control the metabolic activities of the organism. Scattered throughout the endoplasm is a number of granules, these being particles of algæ which the organism uses as food. Finally, a comparatively clear region is frequently visible in the endoplasm. This is the **contractile vacuole,** important in the elimination of liquid waste-products. The whole body is of irregular and incessantly-changing shape, each projection being known as a **pseudopodium.**

Nutrition. *Amœba* lives mainly on minute algæ, which are present on the pond mud which *Amœba* inhabits. During the extension of a pseudopodium it may make contact with such an alga. If it does so the pseudopodium continues to move round on either side of the alga, and thus it is finally completely engulfed. This process is known as ingestion. A drop of water is taken in at the same time as the alga, and the whole constitutes a food vacuole. Once thus inside the body the minute plant is circulated round the endoplasm as a result of *Amœba's* ceaseless motion, and the nourishment is extracted from it by a process of digestion, the endoplasm of the *Amœba* producing such substances as will dissolve the nutritious parts of the alga. Eventually only solid waste matter remains, and this is cast out from any point on the surface of the animal. This process is termed egestion. *Amœba* is said to utilise the carbohydrate and protein material from the plant cell, but it is incapable of assimilating fats.

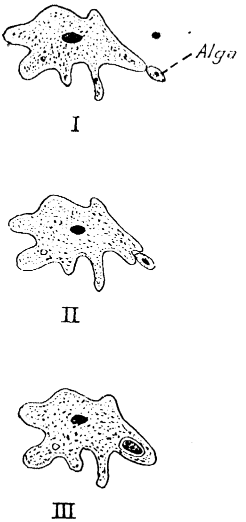


Fig. 2.—*Amœba.* Ingestion.

Locomotion. The extension of pseudopodia by *Amœba* has already been mentioned. But this represents a change only in the shape of the animal, but not in its size. This phenomenon is known as contraction. Thus, by extending pseudopodia successively in a given direction *Amœba* is able to move. As each pseudopodium is extended protoplasm must be withdrawn from other parts of the organism. In such motion the ectoplasm actually moves forwards over the upper surface of the animal in the direction in which the animal is progressing. The movement may be compared with that of a rubber bag filled with water and rolled along over a flat surface.

Respiration. In order to obtain the energy requisite for its life-processes it is essential that *Amœba* should respire. This it does by absorbing through its entire surface the oxygen dissolved in the water in which it lives. As a result oxidation of body-substance takes place and carbon dioxide is formed. This is liberated through the surface of the animal to the surrounding water.

Excretion. It has been pointed out above by what means *Amœba* eliminates its solid and gaseous waste matter: it remains therefore to consider how it deals with liquid waste. This is produced in small droplets throughout the endoplasm, and these droplets ultimately coalesce to form the contractile vacuole. This structure is therefore continuously increasing in size, and eventually, when its maximum size is reached, it contracts suddenly and its contents are expelled to the exterior. The maximum size is determined by a combination of conditions, most important amongst which are surface-tension of the vacuole and the increased pressure exerted upon it by the surrounding protoplasm as a result of its own increase in size. Uric acid has been discovered amongst the contents of the contractile vacuole of forms closely related to *Amœba*. But this is probably not the sole function of the contractile vacuole. The protoplasm of which the body of *Amœba* is made up contains mineral salts in solution, this solution being more concentrated than the surrounding water. Accordingly water will tend to flow into the body of *Amœba*, the surface of which may well act as a semi-permeable membrane. The contractile vacuole affords a mechanism whereby this excess water may be eliminated, the water having picked up the soluble nitrogenous waste matter during its passage through the endoplasm. The absence of contractile vacuoles in marine forms renders this hypothesis even more probable, for there the concentration of salts in the sea-water would inhibit the setting up of an osmotic pressure within the animal.

Irritability. The ability to respond to stimuli is one of the characteristic properties of living matter, and is well shown in *Amœba*. It has already been observed that a pseudopodium, on making contact with an alga, flows round it and finally engulfs it. But if the alga be replaced by a foreign particle—e.g. a grain of sand—the pseudopodium is immediately retracted, and a fresh one is put out in another direction. *Amœba* may, however, be found to engulf even such foreign particles if they are in motion. This is probably because the algæ on which it lives are usually provided with a flagellum, which renders them motile. Again, if a small electric current be passed through water containing an *Amœba*, retraction of all pseudopodia occurs. Thus *Amœba* demonstrates the property of differential irritability in that it not only responds to stimuli, but varies its response, though naturally to a limited extent, to different types of stimuli. Beginnings of conductivity are also shown, for, on retracting one pseudopodium from an obstruction, it extends one in another direction.

Reproduction. *Amœba* differs from higher animals in that at no time is the process of growth exactly neutralised by that of wear and tear, so the organism must be continuously increasing in size.

But as this occurs the ratio of surface-area to volume of the animal must decrease, and eventually it reaches a minimum. This is readily comprehended when it is remembered that all the life-processes above described involve the surface, and respiration in particular must suffer as the area becomes relatively reduced. Accordingly it is found that the organism splits into two halves, identical with the parent in all but size. First in this process the nucleus divides into two, the two halves separating. The cytoplasm —i.e. endoplasm and ectoplasm—then becomes constricted between these two nuclei (daughter nuclei, as they are called), and finally there remain two masses of cytoplasm each with its nucleus. In this way two new individuals are formed as a result of the division of the parent. This process is known as binary fission, and, so long as the conditions remain favourable, *Amœba* is potentially immortal. But even in its secluded habitat climatic conditions sometimes make it expedient for *Amœba* to adopt another means of survival. This is by encystment. When this occurs all the pseudopodia are withdrawn, and a comparatively resistant coat is formed to enclose this rounded mass of protoplasm. Within this cyst the nucleus divides many times, and around each fragment is collected a small portion of cytoplasm. As many as 600 such bodies may thus be formed, and each is termed a spore. When conditions become favourable again the cyst wall becomes dissolved, and the spores are liberated, the residual cytoplasm dying off. Each spore eventually matures into a new *Amœba.*

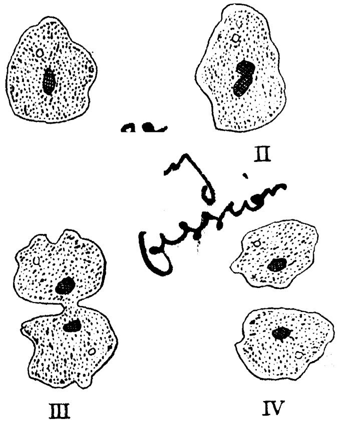


Fig. 3.—*Amœba.* Binary fission.

Thus *Amœba,* with such limited structures at its disposal, is able to carry out the majority of the life-processes which are associated with the higher animals, and only in its method of reproduction, wherein the reproducing organism sacrifices its individual existence, does it differ markedly from them.

(2) EUGLENA

Euglena also belongs to the phylum Protozoa, but it is especially interesting on account of its possession of chlorophyll, a charthe surface, the oxygen dissolved in the water diffusing into the body and the waste carbon dioxide escaping in a similar manner.

Excretion. Liquid waste matter contributes to the formative vacuoles, which discharge their contents into the contractile vacuole. On reaching its maximum size this closes suddenly to expel excretory fluid through the pellicle, specially weakened at that spot for the purpose. When this has been effected the formative vacuoles coalesce to form a new contractile vacuole, whilst new contributory ones soon appear as narrow slits radiating from it.

Irritability. *Paramecium*, on coming into contact, during progression, with a foreign body, is found momentarily to move in the opposite direction. This movement is effected by a reversal of the cilia-beat. Immediately afterwards the organism becomes slightly rotated about its centre and then moves forward in the changed direction. This change of direction is brought about by the differential beating of the cilia on the two sides of the animal. The whole sequence of movements above described is known as the "avoiding reaction," but, as will be seen later, it is only imperfectly adapted to protecting the organism from dangerous substances. Let it be imagined that a drop of dilute salt-solution (about ½%) be placed by means of a very fine pipette into a drop of *Paramecium* culture on a microscope slide. This drop of solution remains empty of *Paramecia*, the animals effecting the avoiding reaction when they come into contact with it. But if this salt-solution be replaced by acetic acid (about 0·02%) then the *Paramecia* are found to pass into the drop of acid and are unable to escape from it. This is because, once inside, the avoiding reaction is performed on reaching the surface of the water, and thus the animals are retained within the acid, where they quickly perish. Thus in this case the avoiding reaction works their doom. Such a forced reaction to a given stimulus as that seen in the avoiding reaction of *Paramecium* is called a **tropism.** *Paramecium* also responds to various conditions of temperature. If one end of a glass slide containing *Paramecium* culture be heated to 40° C. and the other maintained at 25° C. it is found that the organisms collect at the cooler end. On the other hand, if the temperature of the end at 40° C. is reduced to 10° C. they continue to collect at the end at 25° C. This would appear to be their optimum temperature, and the organisms are prevented from leaving it by performing the avoiding reaction when tending to move into a hotter or colder region. In an exactly similar way *Paramecium* is enabled to select a moderately illuminated region of its environment in preference to an intense light. A somewhat artificial instance of response to stimulus by *Paramecium* may be demonstrated by passing a minute electric current through a culture. It is found that the organisms tend to move in the direction of the positive ions, as can be verified by reversing the direction of the current.

Reproduction. In healthy cultures a process of binary fission occurs two or three times a day. The meganucleus and the micronucleus each divide into two, the halves moving apart. Thereafter the cytoplasm becomes transversely constricted, and as a result two daughter individuals are formed, but each with an incomplete set of contents, e.g. each has only one contractile vacuole. There follows, then, a process of growth and development, wherein each product of fission comes to resemble the parent.

Conjugation. It is often observed that simple binary fission in *Paramecium* gives place to a much more complicated phase in the life-history, known as conjugation. In this process two individuals are concerned, and they come together by their ventral surfaces, which themselves become connected by a narrow protoplasmic bridge. The micronucleus divides twice in each conjugant, thus forming four nuclei. Three of them remain inactive, whilst the fourth divides again, so that at this stage each conjugant contains two active nuclei. Of these latter one passes from each conjugant into the partner, so that there is effected an exchange of nuclear material. The nucleus from each conjugant passing into the other is termed the migratory nucleus, whilst the one remaining in the conjugant in which it was formed is described as stationary. Thus, although there is no apparent difference between these two nuclei they exhibit a physiological differentiation characteristic of the two sexes throughout the animal- and plant-kingdoms, for the male element is typically active, whereas the female counterpart remains passive. Accordingly the migratory nuclei may be regarded as representing the male, and the stationary nuclei the female, factors in the reproduction of *Paramecium*. At this stage a further point of similarity to the process of sexual reproduction in higher animals occurs, for the migratory nucleus of each conjugant, having passed into the other partner, fuses with the stationary nucleus of the latter. This fusion of nuclei is characteristic of sexual reproduction. Thus the body of each conjugant becomes a true zygote. At this stage the conjugants separate, and the meganucleus of each disintegrates and disappears. The fused nucleus in each ex-conjugant now divides three times to form eight small nuclei, three of which become resorbed into the cytoplasm. Now the cytoplasm of each ex-conjugant becomes constricted into two halves. Four of the five nuclei undergo no further division, but the fifth divides at the same time as the cytoplasm, so that each new mass of cytoplasm contains three nuclei—two of the undividing four and one product of division of the fifth. This same nucleus now divides again in each cell, and again the cytoplasm becomes constricted, so that each mass now contains one of the four undividing nuclei and one product of division of the fifth. The former becomes the meganucleus and the latter the micronucleus of a new *Paramecium*. Since these two divisions occur in both ex-conjugants a total of eight new individuals is formed as the result of the process of conjugation.

There are conflicting ideas regarding the explanation of conjugation, but the process obviously results in the rejuvenation of nuclear material, since a new meganucleus is formed as a result of repeated division of a composite nucleus formed in each conjugant.

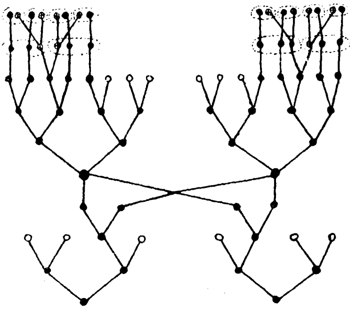


FIG. 7.—Diagram to show behaviour of micronuclei in conjugation. Nuclei left clear disappear.

Weismann maintained that all Protozoa, under suitable conditions, could go on dividing asexually for ever. Calkins, however, suggested a rhythm of activity and depression in *Paramecium*, asexual reproduction giving place to conjugation when the stock became senescent. But he affirmed that this period of depression prior to conjugation could be overcome by a change in the medium, e.g. in food supplied. Later views, however, seem to see the accumulation of waste matter in the meganucleus as a controlling factor, and the postulation of a rhythmic cycle is largely discountenanced. The essential object of conjugation would, then, appear to be nuclear reconstruction—known as **endomixis.**/ When the food supplied to a culture of *Paramecia* is changed the meganucleus disappears, and is reformed from a product of division of the micronucleus. No conjugation then occurs, the same result having been effected by other means. It is claimed that frequent changes of diet cause periods of depression to follow each other progressively more rapidly.

It will be evident, therefore, that reproduction in the Protozoa, exemplified for this purpose by *Paramecium*, can be effected only by fission. Any form of fusion must result in *decrease* of numbers, and not increase. Thus the process of conjugation must have some other significance, and this, as has been stated, is probably nuclear reconstruction. Numbers are increased in this process only by subsequent fission, which is merely incidental to the conjugation. In higher forms this phenomenon of **syngamy** (fusion of gametes) results in multiplication of the species merely because the gametes can be liberated from the parents, which do not, therefore, have to sacrifice their own individual existence. But reproduction and sexual fusion remain fundamentally opposed.

CHAPTER III

MONOCYSTIS

AMONGST the reproductive organs of the earthworm is a number of large sacs, known as vesiculæ seminales, in which the sperms, liberated from the testes, ripen. The cavities of these sacs are frequently inhabited by a parasitic Protozoön known as *Monocystis.* It should be at once realised that a parasite is an organism depending for its existence on an individual living host. It is not sufficient, in accordance with the usual definition, to say that it is an organism subsisting on living matter. This definition is inaccurate for two reasons. First, an animal may be a parasite without subsisting on living matter. An example of such is the tape-worm, which may infest the intestine of man and other mammals, where it absorbs the digested food through its entire surface and does not utilise living matter as its food. Second, an organism may subsist on living matter yet not be a parasite. A cow fed exclusively on living pasture could not in consequence be designated as a parasite.

Structure. There are normally found together two species of *Monocystis*, known respectively as *Monocystis magna* and *Monocystis agilis*. *Monocystis magna*, as its name suggests, is the larger of the two, and is actually visible to the naked eye, living normally attached to the inner surface of the seminal vesicle. The other species lives freely in the cavity of this organ. The bodies of members of both species are long and narrow, with the cytoplasm clearly differentiated into an ectoplasm and an inner, granular endoplasm. The surface is covered with a cuticle, beneath which is a contractile layer—the **myocyte**—, whilst at one end the cuticle is modified into a knob-like structure, known as the **epimerite,** by means of which attachment to a host cell may be effected. The nucleus is large

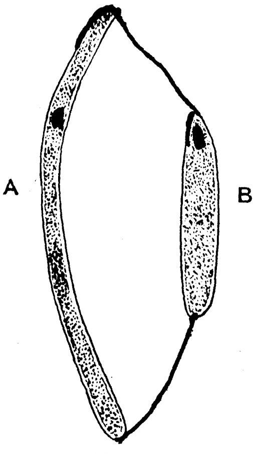


FIG. 8.
A, *Monocystis magna.*
B, *Monocystis agilis.*

and vesicular, whilst the endoplasm contains a great deal of paraglycogen (carbohydrate material allied to starch). There is no contractile vacuole present.

Nutrition. *Monocystis* takes as food the nutrient fluid intended for the ripening spermatozoa, absorbing it through the entire surface.

Respiration and Excretion. Being thus enclosed within the body of their host the parasites have no access to free oxygen. Accordingly, they must obtain their requisite energy as a result of a process of fermentation, whereby body-substance, and, in particular, carbohydrate material, is partially oxidised, a reaction involving the liberation of energy. Since no contractile vacuole is present the waste matter produced must escape in solution by diffusion through the surface.

Locomotion. Owing to the presence of a cuticle no pseudopodia may be formed. By means of the myocyte, however, slow waves of contraction pass along the body, and the *agilis* species is in this way able to effect some movement.

Life-history. The adult form above described is known as the **trophozoite,** and its body is bordered by a fringe of sperm-tails. These trophozoites eventually pair off, each pair becoming surrounded by a cyst. No fusion occurs at this stage, but the members of each pair undergo multiple fission in much the same manner as the encysted *Amœba,* so that there is left behind a small mass of residual protoplasm. This is largely used up in nourishing the products of fission. These small cells conjugate in pairs, and it is affirmed that the members of each uniting pair are derived from different parent cells. This process of fusion of cells derived from different parents is known as cross-fertilisation, and is the general rule in both animals and plants. Only rarely does self-fertilisation occur, this process being characterised by the fusion of cells derived from the same parent. It is even claimed that in the *agilis* species the uniting cells differ in appearance, one being rounded and the other conical in shape. Each zygote (the product of fusion of two germ-cells) surrounds itself with a cyst, and in this state becomes known as a **pseudonavicella,** the living contents of the cyst being a **sporont.** Each sporont then undergoes three successive divisions to form eight minute **sporozoites.** Thus, at this stage there is present one comparatively large cyst containing many smaller capsules, in

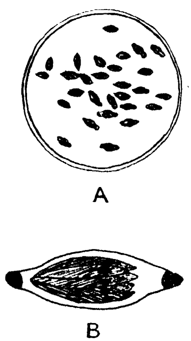


Fig. 9.—Stages in life-history of *Monocystis.*
A, Cyst.
B, Pseudonavicella.

each of which may be found eight sporozoites. The problem now confronting the parasite is the infection of another earthworm. No further development of the sporozoites occurs until they have escaped from their present host. This is normally effected by the latter's being eaten by a bird. The sporozoites are well protected by horny cases from the destructive action of the digestive juices of the bird, and are thus eventually cast out into the soil with the fæces. This soil may then be eaten by another worm, and this time, owing to the particular nature of the worm's digestive juices, the cysts are dissolved and the sporozoites liberated. Each then bores its way through the tissues of its new host until reaching the vesiculæ seminales. Here it penetrates a sperm-mother cell (a cell which, by division and differentiation, would have eventually given rise to sperms), and, feeding upon the protoplasm which this cell contains, eventually becomes a trophozoite. Thus the life-history may be summarised as follows—

2 trophozoites → x pairs of fusing cells → x sporonts →
→ x pseudonavicellæ → 8x sporozoites.

How many of these latter eventually form new trophozoites will obviously depend on whether or not they reach a new host.

Thus, as in parasites in general, the chief problem of survival is to ensure the infection of new hosts. This is done mainly by producing as large a number as possible of "germs" for distribution. Accordingly, we find two multiplicative phases in *Monocystis*—

(i) The paired trophozoites divide many times prior to fusion of gametes.
(ii) Each sporont divides to form eight sporozoites.

In the case of *Monocystis* no development occurs in the gut of the bird, but forms will be studied later (e.g. *Distomum* and *Tœnia*) in which an essential part of the life-cycle is carried out in some intermediate host.

The Protozoa. The Protozoa are non-cellular animals, and they are divisible into four classes. The class Rhizopoda, exemplified by *Amœba*, contains those forms whose locomotion is effected by means of pseudopodia. The Flagellata, known also as the Mastigophora, move by means of flagella, as seen in *Euglena*. *Paramecium* is a member of the class Ciliata or Infusoria, characterised by the presence of cilia to effect locomotion. There are usually two nuclei present. The remaining class, the Sporozoa, is somewhat artificial, for in it are included the majority of the parasitic forms. Their life-history is usually complicated, whilst external organs of locomotion are absent. Members of this class are probably derived from the other classes, but have become modified in adaptation to a parasitic mode of life.

CHAPTER IV

HYDRA AND OBELIA

Hydra and *Obelia* belong to the group of animals known as the Cœlenterata. The chief characteristic of members of this phylum is that their bodies are essentially sacs, bordered by a double wall, and with only one aperture leading from the body-cavity to the exterior. The diagnostic features of this phylum may best be ascertained by a detailed study of two of its members.

HYDRA

Structure. *Hydra* lives in fresh-water, chiefly in ponds and ditches, where it is found attached to a substratum of water-weeds. It is visible to the naked eye, but may be found in either an expanded or contracted condition. Like all members of the group its body consists of a hollow sac, bounded by two single layers of cells. These are the **ectoderm** on the outside, and the **endoderm** bordering the body-cavity or **enteron**. This latter communicates with the exterior by a **mouth**, situated at the free extremity of the animal on a projecting **hypostome**, and surrounded by a ring of some eight **tentacles.** These are evaginations of the body-wall of the animal, and are therefore two-layered, the enteron also extending for some distance into each. Separating the two layers of the body is a gelatinous, non-cellular **mesoglœa.** It may frequently be possible to distinguish a small branch or bud on such an individual, resembling it in all but size. Not far behind the tentacles in a mature

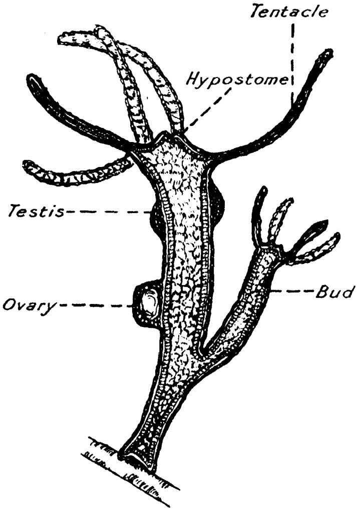


FIG. 10.—*Hydra*, seen in longitudinal section.

individual are lateral swellings. These are the **testes.** Nearer to the attached end is an **ovary,** which eventually gives rise to a single ripe ovum.

Layers of the Body. The ectoderm consists principally of two types of cell. The **musculo-epithelial** cells are large and cover practically the entire surface. The epithelial portion of each cell is wide towards the outside but tapers on passing inwards. At its inner extremity it is expanded to form a number of muscular processes. These processes from all the cells form an almost continuous layer all round the animal just beneath the surface. Tapering as they do towards their inner ends it follows that spaces must occur between these parts of the musculo-epithelial cells. Each such space is occupied by an **interstitial** cell. These are markedly undifferentiated, and it is said that if the occasion arises they are able to give rise to any of the remaining types of cell in the animal. The whole ectodermal surface is covered with a pellicle except at the region of attachment, known as the foot or disc, and here an adhesive substance is produced to ensure firm anchorage. Embedded at intervals in the ectoderm, and especially in the tentacles, is a number of small, specialised cells known as **cnidoblasts.** Groups of them may be found together, forming batteries. Each cell is conical in shape, with the narrow end directed towards the surface. Close to its aperture is a small, sensitive process, termed a **cnidocil.** In each cnidoblast is a cavity, known as a **nematocyst,** opening near the cnidocil. Contained in this nematocyst is a coiled thread embedded in a fluid, whilst the wall of the cavity contains a specially contractile layer of protoplasm. When the cnidocil is touched the thread is expelled. These threads vary in length, being sometimes long and barbed at the tip, and in other nematocysts they are shorter and without barbs. Nematocysts are chiefly of use in the capture of food, for the long barbed

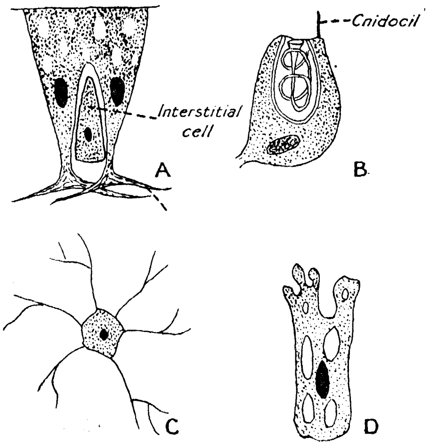


FIG. 11.—Histology of *Hydra*.
A, Musculo-epithelial cells.
B, Cnidoblast.
C, Nerve-cell.
D, Endoderm cell.

threads first wound the prey which is then held firmly to the tentacles by the shorter threads, so that it can be conveyed to the mouth. Another function of the ectoderm is the formation of the germ-cells. Ectoderm cells are also modified to form nerve cells, which become sunk into the mesoglœa. Each is very much branched, and by contact between neighbouring cells a nervous network is formed throughout the whole mesoglœa. It is claimed that specialised sense-cells extend at intervals from this layer through the ordinary ectoderm up to the surface.

The endoderm cells are of much more uniform structure. They are cylindrical in shape, but the bulk of them are subdivided at the ends projecting into the enteron. Others, particularly in the region of the tentacles and mouth, are of regular shape and are glandular. The bases of all these cells are expanded into contractile processes which run transversely around the body, and not longitudinally as do those of the ectoderm. The cells themselves are vacuolated and frequently contain small, rounded bodies, green in colour owing to the possession of chlorophyll.

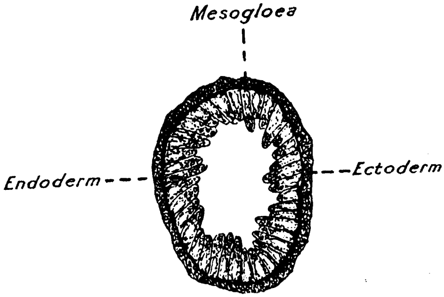


FIG. 12.—*Hydra*—transverse section.

Nutrition. *Hydra* lives principally on water-fleas, captured by the tentacles in the manner already described, and then conveyed to the mouth. Here the food is treated in two ways. A certain amount of it is digested by juices produced in the glandular cells of the endoderm, whilst some of it is actually ingested by the projections of the endoderm cells. These flow round and engulf food particles in much the same manner as is effected by the pseudopodia of *Amœba*. The digested food is absorbed in solution by the endoderm cells. The green bodies contained in the endoderm are not without significance in the process of nutrition. Containing chlorophyll they are able to effect photosynthesis, the sugars thus formed being assimilated by the animal. Solid waste matter from the enteron must be expelled to the exterior through the mouth.

Respiration. There are no special respiratory organs in *Hydra*, so that the respiration must be effected by a process of gaseous exchange through the surface of the body. Since *Hydra* lives an attached mode of life there is not that same demand for energy as in most animals.

Excretion. Liquid waste matter is probably eliminated partly through the surface and partly by being exuded from the vacuoles of the endoderm cells into the enteron, from whence it is expelled, together with the solid waste, through the mouth by the contraction of the body.

Locomotion. Though normally a sessile organism *Hydra* is able, when occasion arises, to change its position to a limited extent. This it does by bending over and affixing its tentacles to the ground and then releasing its disc, which it may reattach nearer to the tentacles, or even swing right over and fasten down on the opposite side of the tentacles. In either case the tentacles then resume their normal function when the disc has become again attached to the substratum.

Reproduction. This is effected in two ways, for it is possible for a considerable number of daughter individuals to be formed from a single parent by a process of budding. At a point usually in the lower half of the animal both layers of the body-wall become evaginated, so that a hollow bud is formed, into which extends the enteron. The bud is originated by a multiplication of interstitial cells, which subsequently become differentiated into the various types of ectoderm and endoderm cells. By a similar process of evagination tentacles are formed at the free end, in the midst of which a mouth becomes perforated. Several buds may be formed simultaneously, and it is even possible for secondary buds to be produced before the first is liberated from the parent. This latter process eventually takes place by a constriction at the base of the bud, which, after being set free, soon attaches itself to a water-weed or other suitable object. Occasionally *Hydra* may reproduce asexually by a division of the whole body, either transversely or longitudinally, into two parts, each of which must develop new structures. Akin to the process of asexual reproduction is the power of *Hydra* to effect regeneration. If a *Hydra* be cut into pieces any portion not less in size than a certain quite small minimum will grow into a complete animal.

Sexual reproduction frequently occurs in *Hydra*. The ovaries and testes are both originated by rapid multiplication of interstitial cells. In the ovary one of these cells soon becomes noticeably larger than the remainder, extending pseudopodia wherewith it engulfs the surrounding cells. In this way it acquires a good supply of reserve food and soon bursts through the musculo-epithelial covering in that region to be exposed on the surface of the animal, save for a thin, gelatinous coat. In the testes a very large number of spermatozoa is produced, and they are soon liberated into the water. Presently one such spermatozoön may come into contact with an egg-cell, with which it then fuses to form a zygote. This undergoes cleavage to form a hollow blastula, into the cavity of which cells migrate to form a two-layered sac, though the endoderm soon becomes solid. The ectoderm now secretes a horny capsule about itself, so that a period of rest ensues, the embryo falling away from the parent. This capsule later bursts and the embryo emerges. An enteron appears in the midst of the endoderm and a mouth is perforated, whilst tentacles begin to form. Attachment quickly follows and the organism goes on to reach maturity.

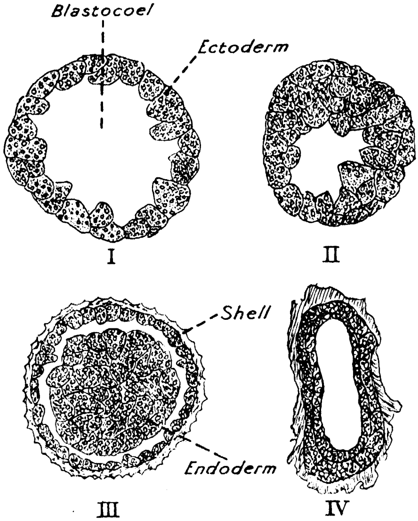


FIG. 13.—Stages in the development of *Hydra*.

OBELIA

Obelia, which lives attached to sea-weed near low water-mark, is a colony of *Hydra*-like organisms, and in structure it may be regarded as a *Hydra* which has undergone repeated budding, but the buds have not become separated from the parent.

Structure. The budding above referred to must be visualised as having taken place regularly, so that there is produced an orderly arrangement of **polyps,** as the separate *Hydra*-like structures are called, on a common stalk—the **hydrocaulus.** These polyps are of two kinds, known respectively as **hydranths** and **blastostyles.** The hydranths are comparatively numerous, and each is very like a *Hydra* in appearance. It is distinguishable from it by the fact that the tentacles are solid, being filled with large endoderm cells, and there are more of them than in *Hydra.* The muscular fibres of the musculo-epithelial cells of *Hydra* have, in *Obelia*, become completely propelled forwards, ex-umbrellar surface first. It would appear at first sight that this medusa is quite unlike a hydranth in structure. But if it be imagined that the manubrium corresponds to the hypostome of the hydranth, then, if the hydranth be longitudinally compressed and transversely expanded, a structure very like a medusa would be formed, assuming that the enteron were closed save for four canals, joined round the margin of the disc. But the principal significance of the medusa is its method of reproduction. It reproduces sexually, and every medusa gives rise to either spermatozoa or ova, but not both, so that the sexes are separate. The germ-mother cells are formed in the ectoderm of the manubrium and are passed *viâ* the gullet to the radial canals. About half-way along each of these the germ-cells penetrate to the ectoderm of the sub-umbrella, where they develop into gonads—either ovaries or testes. Thus there is one gonad on each radial canal. On reaching maturity the walls of the gonads burst, and both eggs and sperms are shed into the surrounding water, where fertilisation of an egg results in the production of a zygote. Development of this proceeds in much the same way as in *Hydra*. By segmentation a hollow blastula is first formed, the cavity of which becomes obliterated by invasion of cells from the bordering wall to form a mass of solid endoderm. Later a split appears in this, but, instead of settling down at this point, as does *Hydra*, the ectoderm becomes ciliated and the larva swims actively about. It is known as a **Planula.** This period of activity is short, however, and soon a resting stage is formed. This becomes attached at one end, whilst the other becomes perforated to form a mouth, around which tentacles appear. The polyp thus produced commences to bud in a regular manner, and in this way a new colony is formed.

Alternation of Generations. It is apparent, then, that there are found here two methods of reproduction—sexual and asexual. This is frequently the case with the lower animals, and the general rule throughout the whole plant-kingdom, but in *Obelia*, as in plants, these two methods of reproduction follow each other in regular sequence. Thus there is produced, by development of the fertilised egg of *Obelia*, a hydranth which reproduces asexually to form an entire colony. When this reaches maturity it forms blastostyles, from which medusæ are liberated. These now proceed to reproduce sexually, the fertilised egg so formed giving rise to new hydranths. This process may be very closely compared to that taking place in plants—Angiosperms, for example. The *Obelia* colony may be said to correspond to the sporophyte generation of the angiosperm—the conspicuous generation producing the flower. The *Obelia* colony eventually gives rise to medusæ of two sorts, namely male and female. The flower performs an analogous function, for it produces pollen-grains and ovules, which undergo development to form respectively the male and female gametophyte generations. The matured ovules and germinated pollen-grains thus correspond to the female and male medusæ of *Obelia*. From these structures germ-cells are produced. The male medusa forms spermatozoa, and in the matured grain develops a male generative nucleus, whilst the female medusa produces eggs, an egg-cell also being set aside in the embryo sac when the ovule ripens. At this stage fertilisation must occur in both *Obelia* and the plant. The fertilised egg thus formed develops into a new *Obelia* colony or a plant sporophyte. But if this process of alternation of generations is so well marked in *Obelia*, how can its absence in the closely-related *Hydra* be accounted for ? To this there are two possible answers. Either *Hydra* has not progressed so far as *Obelia* from an evolutionary point of view, and thus has not yet developed a medusoid form, or else, descending from an *Obelia*-like stock which had one, it has become degenerate. No dogmatic choice can be made between these two alternatives, but the possibility of the degeneracy seems more likely. This is borne out by the fact that in a form somewhat similar to *Hydra*, known as *Tubularia*, a vestigial medusa is formed, but is never liberated from the parent hydranth. It functions to produce germ-cells, which fuse to form fertilised eggs. These develop *in situ*, and it is not until actual larvæ are formed that they are set free. Now the question arises as to whether this medusa is a vestigial—i.e. evolutionarily under-developed—or degenerate—i.e. undergoing evolutionary destruction—structure. A partially developed medusa is of no use to any Cœlenterate, for in its complete form it obviously functions to effect distribution. The fully-grown animal is sessile, and therefore only by this medusa and a planula larva can the species be distributed. A medusa which is never liberated is of no service in this respect, and thus it is inconceivable that the formation of an attached medusa represents a stage midway between the development of no medusa and the formation of a free-swimming one. Far more likely does it represent an intermediate stage between a free-living medusa and the total loss of one. *Hydra* may well represent this last stage where with no medusa being formed, the property of producing germ-cells has been delegated to the hydranth. Other forms are known in which the medusa is even more degenerate than in *Tubularia* being little more than a sac containing the gonads. On the other hand, evolution has taken place in the opposite direction in other members of the Cœlenterata, the hydroid polyp having become more or less completely suppressed, the medusa being the only conspicuous form. This is the case with the common jelly-fish, *Aurelia aurita*, which is simply a large medusa.

Division of Labour. It was observed in studying *Amœba* that this non-cellular organism was able to carry out all its own life-processes with such limited structures at its disposal. Higher animals are found to be divided up into cells. When this first occurred there were two possibilities open to these new organisms. Either every cell was to retain the ability to perform every life-process for itself and thus remain independent of the remainder, or else cells were to become differentiated to perform certain functions to the exclusion of others. This latter was the course adopted, and in consequence there was developed a mutual interdependence amongst the cells. Thus one has become specialised for the production of digestive materials, whereas another may be markedly contractile. Each now depends on the other for successful existence. Thus the organism as a whole is the individual, for the cells function collectively, and an isolated single cell, even if it can be kept alive at all under carefully regulated conditions, leads a pointless existence and in no sense can be deemed an animal organism. This state of affairs is emphasised in the modern biological expression, whereby a multi-cellular organism is described as being divided up into cells, rather than as being composed of a number of cells. A cell may still be regarded as the unit of living matter, but as [illegible] unit of division and not of construction. Further, the Protozoa [illegible] described as non-cellular in preference to unicellular, for th[illegible] former expression stresses the point that there is no division of such an organism into component cells. This differentiation is well shown in *Hydra*. Thus the cells are of varied types, as already described. In the ectoderm are the musculo-epithelial cells, the interstitial cells and the cnidoblasts, whilst the endoderm cells are adapted to the preparation and absorption of food. The interstitial cells remain comparatively unspecialised, and some of them eventually go to form the ova and spermatozoa. It is characteristic of all highly specialised cells that they lose their power of division. Thus germ-cells must always be formed from cells of a primitive type. In *Obelia* this process of division of labour is taken further than in *Hydra*, for not only is the same cellular specialisation observed as in this latter animal, but even the polyps themselves become adapted to serve different purposes. Thus the hydranths are essentially nutritive in function, whilst the blastostyles are concerned with the production of medusæ, and depend for their food on that passed from the hydranths along the hydrocaulus. The medusa itself is on approximately the same plane of organisation as a single hydranth, which it closely resembles

CHAPTER V

DISTOMUM HEPATICUM

Distomum, known popularly as the Liver Fluke, is a parasite frequently inhabiting the bile-duct of sheep fed in damp meadows. It causes the disease known as " liver-rot," which is often fatal.

Externals and Body-wall. In appearance *Distomum* is a brown, flat worm, about an inch in length and half an inch wide. At the front end is a short projection bearing the **anterior sucker,** whilst just behind this, on the under surface, is the **ventral sucker.** In front of this latter is an hermaphrodite **genital pore,** and at the extreme posterior tip is the **excretory pore.** The whole body is covered by a cuticle, from which emerges a number of spines.

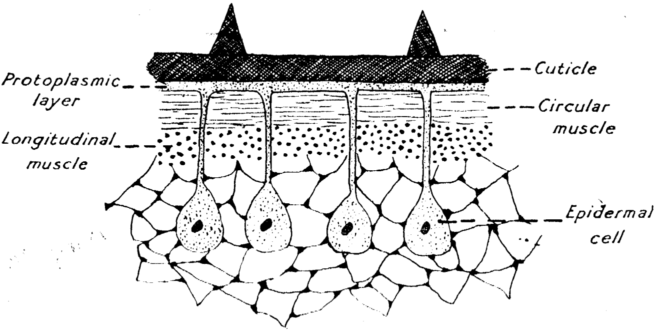


FIG. 18.—*Distomum.* Body-wall.

The cells of the epidermis are sunk some distance into an irregular **parenchyma,** but they retain their connexion with a protoplasmic layer just beneath the cuticle. Between this layer and the parenchyma are circular and longitudinal muscles.

Nutrition. The anterior sucker surrounds the mouth, which leads into a muscular **pharynx.** This bifurcates almost immediately, the two branches running to the extreme posterior end. During their passage these limbs of the gut give off a large number of branches, all of which end blindly. There is no anus, and the food consists of liquids—largely blood—absorbed from the host.

surface of the animal. It is conceivable that sperms from another *Distomum* may enter along this canal.

Life-history. Development is commenced in the uterus, but before long the eggs are shed along the bile-duct into the intestine of the host, and are eventually cast out with the fæces. In moist, warm conditions a larva, known as a **miracidium,** emerges from the egg-case. It is a conical structure covered with large, ciliated epidermal cells. It has a vestigial gut in the form of a pocket at the anterior end : glands open into it near the mouth. In the anterior region is found a " brain," close to which are two eye-spots. The bulk of the larva is of loose, parenchymatous material, and two small excretory tubes (protonephridia), each ending in flame-cells, occur at the hind end. Near the mouth is a large, conical spine projecting forwards. Lying in the parenchyma are two groups of cells which will eventually give rise to ova and sperms respectively. By means of its cilia this larva swims about until meeting a species of fresh-water snail—*Limnœus truncatulus.* With the aid of its spine it bores its way into the " liver " of the snail, where it loses its outer, ciliated layer and all the internal organs except the germ-cells. This hollow sac is known as a **sporocyst.** Cells lining the sporocyst now become detached, and, by a process of parthenogenesis, develop into an independent generation of larvæ—**rediæ.** The germ-cells carried over from the miracidium also produce rediæ. Each redia is an elongated structure with an anterior mouth leading through a muscular pharynx into a short gut. Just behind the pharynx the body-wall is thickened to form the **collar.** At the hind end the body is lined with cells similar to those lining the

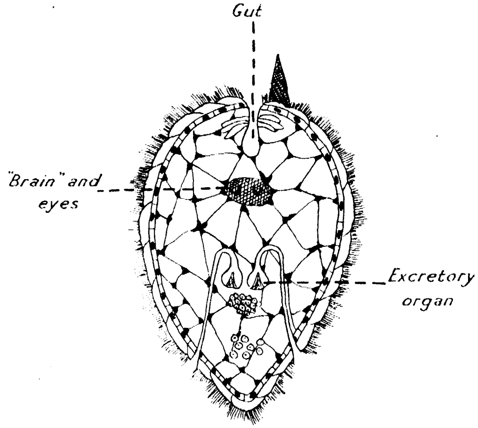


FIG. 23.—*Distomum.* Miracidium larva.

sporocyst, and they behave similarly, developing parthenogenetically into further rediæ. These escape from the parent by an aperture just behind the collar. All these rediæ live on the tissues of the snail, and finally kill it. Several generations of rediæ are thus produced, but eventually a different type of larva is formed, though in a similar manner. This is the **cercaria.** It has an expanded, heart-shaped body, a mouth leading through a pharynx to a bifurcated alimentary canal, an oral and a ventral sucker, and a long tail by means of which it swims. The cercariæ infest the grass, where eventually they lose their tails and become encysted. These cysts are in turn eaten by sheep. In the alimentary canal of the latter the cysts are dissolved, and the cercariæ make their way up the bile-duct to the liver, where they mature into adults.

It will be seen from the above account that a parasite's life-history is considerably complicated in order to ensure, as far as possible, transmission from one host to another. This can be best effected in two ways—

(i) By producing as many larvæ as possible.
(ii) By passing some of the intervening period in an intermediate host.

So far as (i) is concerned it will be seen that in *Distomum* there are three multiplicative phases—

(*a*) The reproductive organs are enormously enlarged so that a very large number of fertilised eggs is produced. Even so it is but very few of them that ever reach the invertebrate host.

(*b*) The germ-cells multiply in the sporocyst and produce rediæ.

(*c*) The rediæ give rise to several further generations of rediæ before they eventually produce cercariæ.

With regard to (ii) it is observed that the miracidia develop no further until they have penetrated the body of the invertebrate host. This provides them with a period of shelter during which rapid reproduction may be effected.

CHAPTER VI

TÆNIA SOLIUM. THE PLATYHELMINTHES

TÆNIA SOLIUM

BELONGING to the phylum Platyhelminthes, or Flatworms, is another parasitic form as well as *Distomum*, known as *Tœnia*, popularly called the Tapeworm from its customary shape. Of this worm there are many species, named according to the host in which they occur. The one for present consideration is *Tœnia solium*, which infests the human intestine.

External Features and Body-wall. As implied by its common name the adult stage of *Tœnia solium* is in the form of a flat worm, attaining a length up to twelve feet. Unlike *Distomum*, but resembling the true worms or Annelida, it is divided up into a large number of segments or **proglottides**—as many as eight hundred and fifty in the fully grown adult. At the extreme anterior end is the head or **scolex.** Arranged round this are four large suckers, whilst projecting from it is the **rostellum**—a process surrounded by a ring of hooks. The suckers and the hooks together effect attachment to the lining of the intestine of the host. Immediately behind the head is a narrow neck, connecting this structure with the chain of proglottides, or **strobila** as it is called. The zone of growth lies just behind the scolex, and from it new proglottides are budded off. Thus the youngest proglottides lie immediately posterior to the neck and the oldest at the extreme hind end. In consequence it is observed that the worm widens posteriorly. The surface is covered with a thick, permeable cuticle, in which small channels occur. Beneath this is a delicate protoplasmic membrane, bordered on the inside by what is known as a basement membrane. The ectodermal cells themselves, as in *Distomum*, have become sunk into an irregular parenchyma. Deeper in the parenchyma may be found a plexus of nerves, enclosed by circular and longitudinal muscles. At intervals dorso-ventral muscles connect the dorsal with the ventral surface. Sense-cells occur in the parenchyma, their processes terminating just beneath the cuticle

Nutrition. *Tœnia solium* is a degenerate organism in so far as it possesses no alimentary canal. Free-living forms belonging to the same class have a well-developed gut, so that this absence of it in *Tænia* may be taken as one of the characteristics of parasitism. The animal is bathed in the digested food of its host, and this it absorbs over its entire surface. There is thus no need for a distributory system in *Tænia*, since the whole surface is capable of absorption. It protects itself from any destructive action of the body-fluids of its host by means of a secretion liberated from a number of lime cells which occur near the bases of the channels passing through the cuticle.

Respiration. Respiration must be of a modified form, since *Tænia* has no access to atmospheric oxygen. Accordingly it takes place by a process of fermentation, carbohydrates in particular being partially broken down, with the formation of complex intermediate products and the liberation of energy.

Excretion. *Tænia* has a well-developed excretory system. Running along on either side of the body is a collecting duct. Each of these receives a large number of tubules from surrounding tissue. These tubules branch profusely, their finest ramifications ending as flame-cells. At the posterior end of each proglottis the two longitudinal collecting ducts are united by a transverse canal. The ducts open to the exterior at the extreme posterior tip of the animal.

Nervous System. The nervous system is surprisingly well developed in view of the fact that, as a parasite, *Tænia* leads a comparatively inactive existence. There is a pair of cerebral ganglia situated in the scolex and joined by the cerebral commissure. These ganglia are connected anteriorly with a nerve-ring in the rostellum, and there are paired dorsal, ventral and lateral nerve-cords running through the entire length of the animal, and joined in each segment by a hoop.

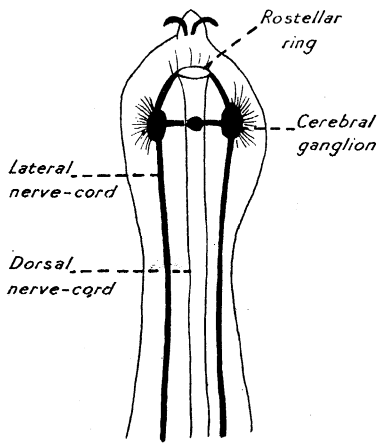


FIG. 24.—*Tænia solium.* Nervous system.

Genital System. Every proglottis has a complete set of reproductive organs, so that the animal is an hermaphrodite. These organs are, of course, mature only in the larger posterior proglottides. There is a diffuse **testis** scattered throughout almost the whole proglottis, the ducts all eventually connecting with a single **sperm-**

larval stages before eventually producing another adult. Some part of development is frequently undergone in an intermediate host, as is demonstrated in *Tœnia.* Other species of *Tœnia* occupy different principal and intermediate hosts. Thus *Tœnia serrata* lives in the dog or cat, and has, as its corresponding alternative intermediate host, the rabbit or mouse. *Tœnia metotica* occurs in birds, the earthworm being the intermediate host. *Tœnia cœnurus* is found in the intestine of certain carnivores, whilst the bladder stage occurs in the brain of sheep, giving them the disease known as "staggers." These last two species are interesting on account of the fact that the bladder-worm multiplies by budding, so that chances of successful propagation are thereby increased.

The Platyhelminthes. It is characteristic of the flatworms that they possess no anus or blood-vessels; their bodies are divisible into three layers (contrast with the Cœlenterata), there is present an excretory system of branched tubes ending in flame-cells, whilst the reproductive organs are complicated and usually hermaphrodite. Members of this phylum are divisible into three classes. The class Turbellaria contains such free-living forms as *Planaria* and *Dendrocœlum.* Locomotion is effected chiefly by cilia. Members of the class Cestoda are endo-parasites and have no alimentary canal, ciliated epidermis or sense-organs. They have organs of attachment, and in development a six-hooked embryo is always formed in an intermediate host, whilst maturity is reached in a vertebrate host. The body is often divided into proglottides. *Tœnia* affords an example of this class. The class Trematoda consists of endo- and ecto-parasites, which have no eyes or ciliated surface. A mouth and alimentary canal are retained, whilst ventral suckers serve for attachment. These characters are well shown in *Distomum.*

CHAPTER VII

LUMBRICUS. NEREIS. THE ANNELIDA

THE earthworm, *Lumbricus terrestris,* belongs to the phylum Annelida, differing from the Platyhelminthes in the possession of a well-defined body-cavity or cœlom.

Habits and External Features. The earthworm inhabits the superficial layer of soil rich in decayed vegetable matter, or humus, rarely occurring at a depth greater than eighteen inches. It lives in a definite burrow, into which such objects as leaves may be drawn, and the opening may be protected by a number of small stones. Earthworms bore their way through the soil, and in so doing they increase the soil's porosity and thus enable water containing dissolved carbon dioxide to reach the solid rock beneath, which consequently becomes partially dissolved, so that these animals contribute not a little to soil formation. The loosening effect exerted by earthworms on the soil increases its penetrability by the roots of plants. The body of an earthworm is divided into about one hundred and fifty segments. It is cylindrical in shape, slightly blunted at the anterior end and dorso-ventrally compressed posteriorly. The dorsal surface is somewhat darker in colour than the ventral, and the whole body is covered with a slime secreted by the cells of the ectoderm. The mouth is situated at the anterior end, being overhung by a short projection known as the **prostomium,** whilst the **anus** occurs at the extreme posterior tip. The first segment, since it surrounds the mouth, is known as the **peristomium.** On every segment except the first and the last are four pairs of short, stiff bristles or **chætæ.** They are arranged as one lateral and one ventral pair on each side of the body, and may be distinguished by passing the thumb and finger in a postero-anterior direction along the body, since they are directed slightly backwards. Besides the structures already described there is a number of important apertures opening on to the surface. On every segment except the first three is a pair of **nephridiopores,** lying just in front of the ventral chætæ : they are the openings of the excretory organs or nephridia. In the mid-dorsal line of the groove behind every segment after and including the eighth is a minute **dorsal pore** leading from the body-cavity or cœlom to the exterior. The fluid (cœlomic fluid) which escapes from these pores assists in keeping the surface of the body moist, besides which the minute, amœboid cells contained in this fluid largely protect the skin of the worm from invasion by ecto-parasites. In each of the depressions between segments 9 and 10 and 10 and 11 there opens ventro-laterally a pair of pocket-like structures known as **spermathecæ,** whilst the **vasa deferentia,** conveying the sperms to the exterior, open as a pair of slits with swollen lips on the ventral surface of segment 15. The pair of openings of the oviducts occur at the same level of the body on segment 14. Covering segments 32–37 is a band of especially glandular skin visible as a swelling in that region and known as the **clitellum,** the significance of which will be considered later.

Body-wall. The whole surface of the body is covered with a thin **cuticle,** a product of the **ectoderm** which lies immediately beneath it. It is perforated at intervals by channels which allow the secretion of the glandular cells of the ectoderm to escape. The ectoderm itself consists of columnar cells, some of which are concerned in the production of a mucous secretion, whilst others are sensitive to certain stimuli. Immediately within the ectoderm is a layer of **circular muscle** circumventing the whole body, and within this again is a layer of **longitudinal muscle.** This is bordered on the inside by a **cœlomic epithelium.** The body of the earthworm may be regarded as consisting of two hollow, concentric cylinders, for within the cylinder already described, and separated from it by a space known as the **cœlom,** containing cœlomic fluid, is the gut or alimentary canal. This is itself enclosed by a layer of **cœlomic epithelium** which, in the region of the intestine, is in the form of large, yellow cells termed the **chloragogenous tissue.** Within this

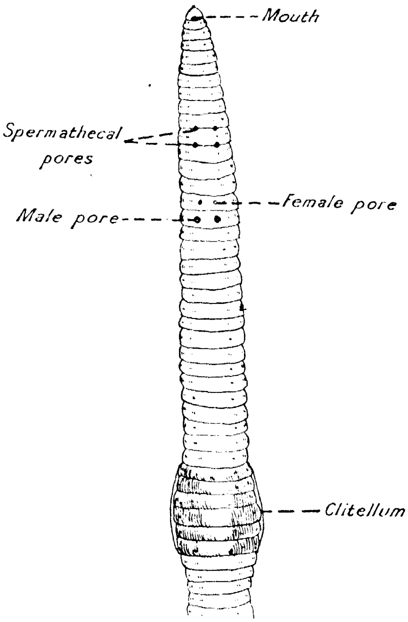


FIG. 27.—*Lumbricus.* Ventral surface.

is a layer of **longitudinal muscle,** followed by a layer of **circular muscle.** The lumen of the gut is bordered by true **endoderm.** It is further observed in the region of the intestine that the dorsal side of the gut is invaginated, the invagination, known as the **typhlosole,** being filled with the chloragogenous cells. In these cells runs the dorsal blood-vessel. The body-cavity or cœlom is interrupted by a number of septa corresponding in position to the grooves dividing the body into segments externally. These septa form a support for the alimentary canal and are perforated also by the blood-vessels, nerve-cord and nephridia.

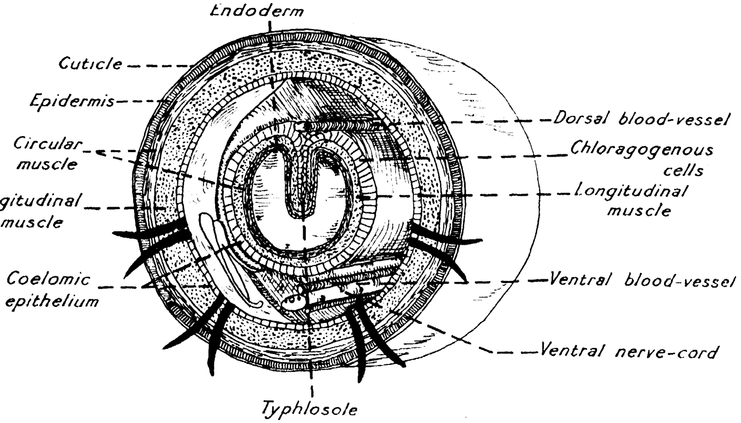


FIG. 28.—*Lumbricus.* Transverse section of segment in intestinal region. (From "Fundamentals of Biology," by J. W. Stork & L. P. W. Renouf.)

Alimentary System. The alimentary canal is a straight tube extending from the mouth to the anus and showing a certain amount of regional differentiation. The mouth opens into a thin-walled buccal cavity occupying the first three segments. This leads into a muscular **pharynx,** situated in the fourth to the sixth segments. The dorsal wall of this region produces a digestive juice which dissolves proteins. The pharynx leads into the **œsophagus,** a narrow, thin-walled tube extending from the seventh to the fourteenth segment. In the twelfth segment are two pairs of lateral **œsophageal glands.** These produce calcium carbonate which is passed into a pair of pouches opening into the gut in the eleventh segment. This calcium carbonate serves to neutralise acids which may enter with the food. In segments 15 and 16 is an expanded **crop** where food may be temporarily stored. From here it is passed into a thick-walled, horny **gizzard** where mastication occurs. The remainder of the gut consists of a thin-walled **intestine,** invaginated to form a typhlosole as already indicated. The chloragogenous cells in this region become loaded with waste matter and eventually fragment into the cœlom, from which their products are eliminated. The inner wall of the intestine produces digestive juices.

In order to get food into its body the earthworm opens its mouth as it bores through the soil. Only the humus of the soil is of any nutritive value, and it is digested and absorbed into the blood-stream of the animal. The undigested remains are cast out of the anus, and these fæces frequently appear on the ground in the form of worm casts. Thus earthworms are of supreme importance to agriculture in that they are continually renewing the surface soil. It has been estimated that an average acre of arable land contains as many as fifty thousand earthworms, each of which is calculated to bring to the surface some twenty ounces of soil in a year. It will be seen therefore that their combined activities must result in the annual raising of nearly twenty-eight tons. In captivity earthworms will eat animal tissues, and particularly fat, this food being drawn into the gut by a sucking action of the pharynx.

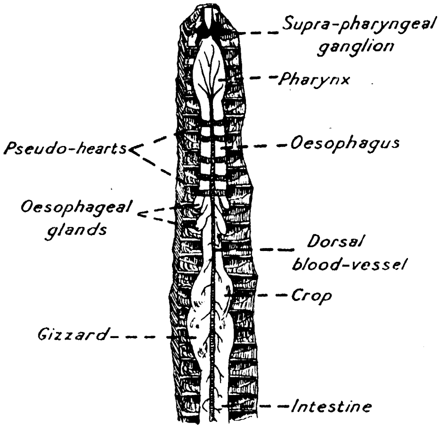


FIG. 29.—*Lumbricus*. Alimentary system.

Vascular System. Unlike forms of animal life below it the earthworm has a well-developed blood-vascular system. There is a large **dorsal** blood-vessel running almost the entire length of the animal and supplying the gut and part of the musculature. In this vessel blood flows forwards, and in each of segments 7 to 11 there arises a pair of contractile vessels, known as **pseudo-hearts,** which connect the dorsal with the **ventral** vessel carrying blood backwards. This latter vessel is concerned principally with supplying the nephridia and the skin, where the blood is purified and re-oxygenated. There is also a **sub-neural** vessel, connected in each segment of the intestinal region with the dorsal vessel by a pair of **parietals.** Blood is maintained in motion by the contractile nature of the dorsal vessel and the pseudo-hearts, whilst there is no possible differentiation of the vessels into arteries and veins. The blood of the earthworm is red in colour owing to the presence of hæmoglobin. This is not confined to corpuscles as in vertebrates, but is contained in solution in the plasma. Colourless corpuscles or leucocytes are also present.

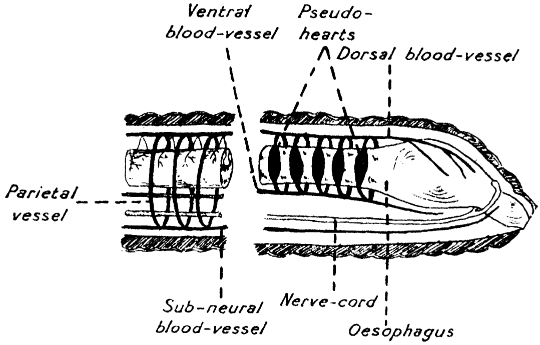


FIG. 30.—*Lumbricus.* Diagram of vascular system.

Respiration. Respiration is effected by gaseous exchange through the surface. It is especially important in this respect that the body be kept moist, for this readily facilitates an exchange. Oxygen absorbed through the skin reaches the blood, principally in the ventral vessel, where the hæmoglobin is oxidised to form oxy-hæmoglobin. This compound dissociates on reaching tissues deficient in oxygen, and the waste carbon dioxide is carried away in solution in the plasma to be expelled through the surface of the animal.

Locomotion. In order to move forwards the earthworm first anchors its hind end by means of the chætæ in that region. It then contracts the circular muscles of the body-wall. This results in an increase in length, since the cross-sectional area must become reduced yet the volume remains unchanged. The animal then attaches its front end by means of chætæ and releases the hind end. The circular muscles are now relaxed and the longitudinal muscles contracted. In consequence the hind end is drawn forwards. By alternately attaching and releasing points nearer together than the extreme front and hind ends any median portion of the animal may thus be extended.

Excretory System. It has already been pointed out that the cavity separating the body-wall from the gut is filled with a fluid. Into this fluid all the liquid waste matter is collected as, for instance, possibly by the disintegration into the cœlom of the chloragogenous cells, though some authorities state that these may be hepatic in function. Some small part of this fluid is exuded through the dorsal pores, but the organs mostly concerned with its purification are the **nephridia,** of which there is a pair in all segments except the first three and the last. A nephridium is a much coiled tube commencing as a ciliated funnel or **nephrostome** just in front of each septum, which it almost immediately penetrates, so that the bulk of the organ lies in the next posterior segment. From this it opens to the exterior by a nephridiopore. The tube itself shows a certain degree of regional specialisation. Just behind the nephrostome is a ciliated tube penetrating the septum. Once in this segment the nephridium continues its course still as a narrow,

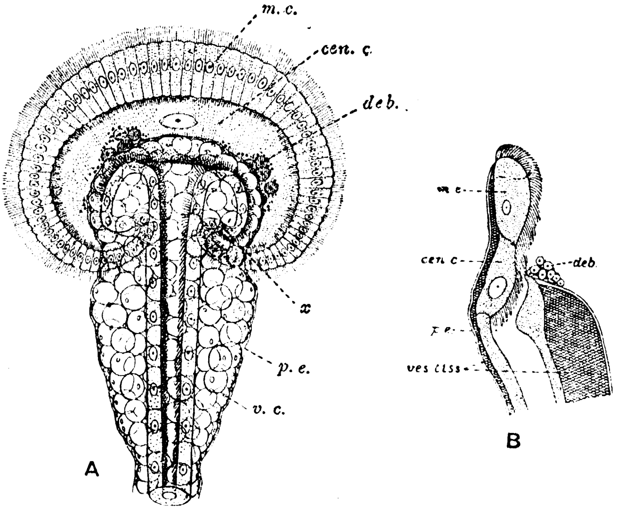


FIG. 31.—Nephrostome or funnel of nephridium of Earthworm. (From "Manual of Zoology," by L. A. Borradaile.) A, In surface view, highly magnified. B, In longitudinal section, diagrammatic.

cen.c., central cell; *deb.*, debris of cœlomic corpuscles and excretory granules; *m.c.*, marginal cell; *p.e.*, peritoneal epithelium; *v.c.*, vesicular connective tissue cells; *x*, point at which marginal cells join lining of tube.

partially ciliated tube, and this gives place to a wider, ciliated, brown tube. This leads into a wider, non-ciliated tube and finally the liquid waste matter is conveyed to the nephridiopore by a much wider, muscular tube. The whole structure is bound together by connective tissue into three distinct hanks, whilst, except in the muscular region, the tube consists of hollow cells joined endwise. The liquids are kept in motion by the beating of the cilia, but the cells constituting a nephridium are actively excretory and not merely passive channels.

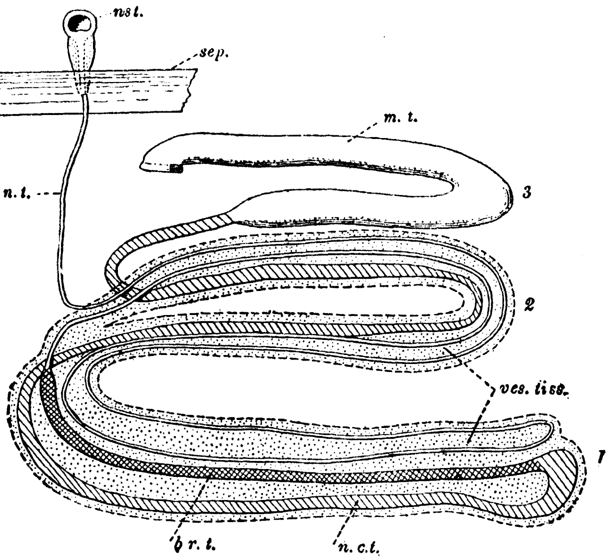


FIG. 32.—Diagram of nephridium of Earthworm. (From "Manual of Zoology," by L. A. Borradaile.)

br.t., brown, ciliated tube; *m.t.*, muscular tube; *n.c.t.*, glandular, non-ciliated tube; *n.t.*, narrow tube, ciliated in parts; *nst.*, nephrostome; *sep.*, septum; *ves. tiss.*, connective tissue; 1, 2, 3, the three hanks of the tube.

Nervous System. The nervous system of the earthworm is well developed. It consists of two **supra-pharyngeal ganglia,** connected by two **peri-pharyngeal commissures** with a double, ventral nerve-cord, which runs throughout the length of the animal. This is expanded in every segment to form a ganglion, from which three pairs of nerves emerge to supply the organs of that segment. The dorsal part of the nerve-cord consists principally of nerve fibres, above the general mass of which are three giant fibres. Each of these consists of a collection of nerve fibres bound in a sheath of connective tissue. Ventrally the nerve-cord is composed mainly of nerve cells. From these cells nerve fibres run to the muscles, and these fibres may therefore be described as efferent or motor, whilst nerve cells just beneath the epidermis are continuous with the fibres visible in the nerve-cord itself and can therefore be regarded as afferent or sensory. The earthworm has no recognised sense organs, but certain of the cells of the ectoderm are prolonged into fibres which reach the nerve-cord. These cells are arranged in groups at the anterior end, forming rudimentary sense organs. Earthworms respond to strong light and are very sensitive to ground vibrations.

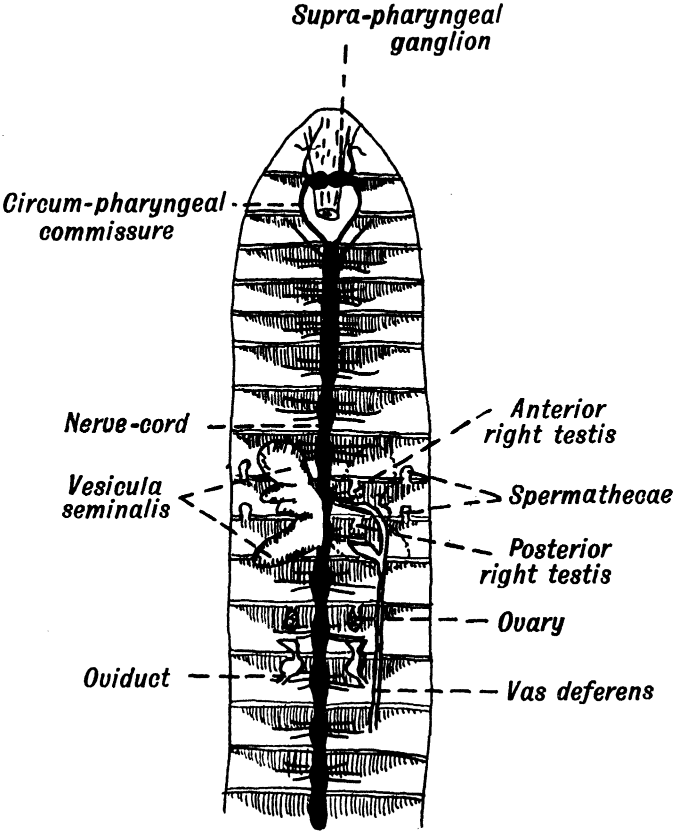


FIG. 33.—*Lumbricus.* Reproductive organs and nervous system. The left vesicula seminalis has been removed.

Reproductive System. *Lumbricus* is an hermaphrodite, i.e. it bears both male and female reproductive organs. The **ovaries** are a pair of pear-shaped bodies situated on the anterior septum of the thirteenth segment. Each is formed by a thickening of the cœlomic epithelium in that region and the eggs produced are cast into the cœlom. From this cavity their only means of escape is *viâ* one of the pair of **oviducal funnels.** These are situated posteriorly in segment 13, penetrating the septum to reach segment 14, where a swelling occurs to form the **egg sac,** and here the eggs are stored. A short oviduct conveys eggs from this sac to the exterior. There are two pairs of **testes** found attached to the anterior septa of segments 10 and 11, and each, as were the ovaries, is a local thickening of cœlomic epithelium. The testes are contained within two pairs of large sacs known as the **vesiculæ seminales.** Each is nothing more than a portion of the cœlom specially walled off for this purpose. The anterior vesicula seminalis, situated in segment 10, is extended into two anterior and two posterior horns, bulging into the ninth and eleventh segments respectively, whilst the posterior seminal vesicle of segment 11 has two posterior horns projecting into the twelfth segment. The sperm-mother cells produced in the testes ripen within these vesiculæ seminales. Each sperm-mother cell divides many times to form a large number of small cells surrounding a mass of residual protoplasm. The body so formed is termed a **cytophore,** and presently the cells mature into spermatozoa. Within each vesicula seminalis is a ciliated funnel, sometimes called a sperm-rosette, leading into a **vas deferens** which soon pierces the wall of the vesicula seminalis. The vasa deferentia thus arising on each side unite and each combined tube opens to the exterior by a pore on the fifteenth segment.

Although an earthworm is an hermaphrodite cross-fertilisation occurs. Pairing takes place under moist, warm conditions, and is prefaced by two worms becoming closely apposed by their ventral surfaces with their anterior ends pointing in opposite directions. They take up such a position that the fifteenth segment of each worm lies approximately against the tenth of the other. Sperms are then liberated from the vasa deferentia of each and are passed into the spermathecæ of the other. This process being completed, the worms separate. An elastic band secreted by the clitellum of each worm then commences to move forwards. On reaching segment 14 it receives from the oviducts the worm's own eggs, and when passing the spermathecæ the "foreign" sperms are discharged into it. Fertilisation of the egg occurs and the whole band and contents are passed forwards over the head. Here the band closes up to form a cocoon. It contains several eggs, only one of which normally completes development. This latter process takes place directly, no larval stage being formed as in most Annelida.

NEREIS

Belonging to the class Polychætæ of the phylum Annelida is a round worm known as *Nereis,* differing from *Lumbricus* in several important respects. It is a free-living, marine form with a large number of species and varying in length from three to nine inches. A common species is *Nereis cultrifer,* found plentifully on the south coast of England, where it leads a sedentary mode of life.

External Features. It is about six inches in length and divided into some eighty segments. It has a highly specialised head region, comprised of prostomium and peristomium, and posteriorly there is a non-segmented **pygidium** enclosing the anus. Two **anal cirri** project backwards from it. Chætæ are much more numerous than in the earthworm, and are borne on structures termed **parapodia.** Each of these is a hollow outgrowth of the body-wall with the cœlom extending into it. It is divisible into two lobes, the dorsal one being known as the **notopodium** and the ventral as the **neuropodium.** Each lobe is further subdivided into **cirrus, ligule** and **chætigerous lobe.** Each chætigerous lobe bears a dorsal and ventral bundle of chætæ, and from each lobe arises an especially stiffened chæta, known as an **aciculum.** All the chætæ, and in particular the aciculum, are provided with muscles to effect movement. Each chæta is derived from a single ectodermal cell by secretion, and new material is added from the base. The chætæ of *Nereis* are described as compound, signifying that each consists of a long shaft into which is set at the distal end a toothed appendage. Owing to the possession of sense organs the anterior end tends to undergo cephalisation. By this it is meant that certain of the anterior segments of the body tend to become incorporated with the head. In *Nereis* this phenomenon affects only the peristomium. At the extreme anterior tip of the head region is a pair of **prostomial tentacles.** Behind these lie two pairs of eyes, each of which is a

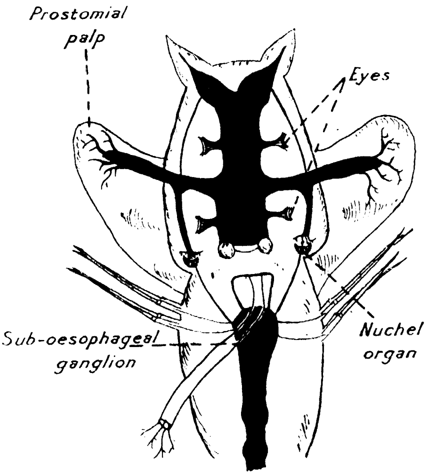


FIG. 34.—Head of *Nereis.*

cup-like structure lined with pigmented, light-sensitive cells and containing a gelatinous mass which functions as a lens. Laterally there are borne two large **prostomial palps** projecting forwards and downwards. Two dorsal depressions at the posterior end of the prostomium form the **Nuchel organs,** of doubtful function. The peristomium bears four pairs of **peristomial cirri,** so that in this way it has become modified from the remainder of the segments behind it.

Body-wall. The body-wall is very like that of *Lumbricus.* There is a cellular ectoderm overlain by a cuticle. Circular and longitudinal muscles occur within it, the latter being divided into four blocks, two dorsal and two ventral. Large groups of gland cells occur at intervals in the ectoderm, especially near the base of the parapodia.

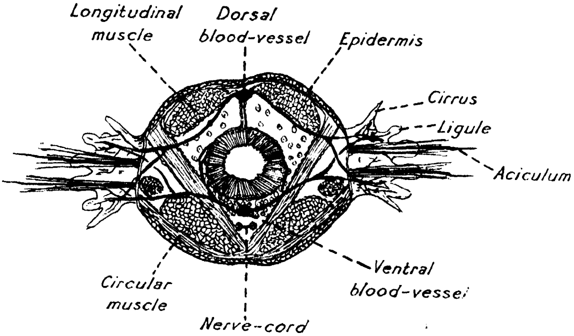


FIG. 35.—Section of segment of *Nereis.*

Internal Anatomy. The alimentary, excretory, nervous and vascular systems are based on the same plan as in the earthworm, but a curious modification of the pharynx is worthy of note. It can be pushed forwards out of the mouth, whilst its lining is cuticularised and specially thickened in places to form a number of teeth and a pair of jaws. The sexes are separate. Ova and spermatozoa are formed from the epithelium lining the blood-vessels at the base of the parapodia, and when ripe are discharged into the cœlom, this process occurring along the whole length of the animal. The genital products escape by bursting through the body-wall, though small, ciliated organs are present just beneath the dorsal bands of longitudinal muscle. These are probably degenerate genital ducts which formerly opened to the exterior. At maturity the entire organism undergoes such remarkable changes that in this state it was erroneously identified as another genus and called *Heteronereis*. The genital products become collected at the posterior end, eating ceases, the body-wall becomes thin and the alimentary canal is reduced. Most importantly the parapodia and chætæ become modified to form swimming-plates, so that the animal now swims actively about, thus ensuring a reasonable distribution of its genital products.

Development. In development a free-living **trochosphere** larva is first formed, characterised by the possession of cilia arranged in the form of a median ring and a small apical tuft. This becomes gradually converted into the adult form by a process of elongation and segmentation.

The Cœlom. The Platyhelminthes and forms above them (including, therefore, the Annelida) differ from the Cœlenterata in one fundamental property, and that is that the body is divisible into three layers. On the outside is the ectoderm, whilst lining the alimentary canal and its diverticula is the endoderm. Between these two is a mass of tissue described as the mesoderm. In the Platyhelminthes (e.g. *Distomum*) this layer is nothing more than a network of loosely-packed cells, known as the parenchyma, but in the Annelida it has become more highly developed. It constitutes the musculature and the layer of cells enclosing the gut, as well as the muscles surrounding this organ. It is clearly divisible into two layers, separated by a cavity known as the cœlom, and wherever the cœlom occurs it is always in this form. The cœlom is not the only cavity occurring in the mesoderm, however, for the blood-vessels are mesodermal structures, and their cavities constitute the hæmocœl. In some forms—e.g. Insecta—it is practically the only body-cavity existing. The cœlom, where fully developed, is filled with a fluid, known as cœlomic fluid, whilst the two walls are bordered on the cœlomic side by cœlomic epithelium. The functions of the cœlom are—

(1) Since it contains cœlomic fluid it supports the viscera (the soft organs of the trunk), and protects them from shock.

(2) It is the source of the genital products. As has already been pointed out in the case of the earthworm, these are derived from the cœlomic epithelium.

(3) It facilitates excretion. This is particularly obvious in the earthworm, where the nephridia are concerned with the purification of the cœlomic fluid.

It is from this mesodermal layer that the skeletal structures of vertebrates are derived. In accordance with this tripartite division of the layers of the body in all forms above the Cœlenterata they are known as the Triploblastica, whilst the Cœlenterata themselves are the Diploblastica.

Segmentation and Cephalisation. Closely associated with the development of the cœlom in evolution is the appearance of the phenomenon of metameric segmentation. This is essentially the linear repetition of parts, most characteristic amongst which are the gonad pouches, developed from cœlomic epithelium. In many Annelida, including *Nereis*, gonads are produced in every segment throughout the length of the animal. In the earthworm this primitive condition no longer obtains, for the gonads are restricted to a few segments in the anterior region of the body. Thus metameric segmentation is essentially a cœlomic property, and takes place in all those animals possessing a cœlom. It must be carefully distinguished from the type of segmentation found in the Platyhelminthes, e.g. *Tœnia*. Here the linear repetition of parts is brought about by a process of budding, or strobilisation, and is not confined to the cœlom or gonads. The proglottides of *Tœnia* possess an independence which cannot possibly exist in the case of the segments of an Annelidan.

In most animals above the Annelida there is a specialised region known as the head. It becomes particularly well differentiated in respect of the nervous system, the nerve-cord becoming enlarged to form the brain. In consequence a number of segments becomes incorporated in the head, and this phenomenon is known as cephalisation. It takes place to such an extent and so completely that it is difficult in some cases to observe any segmentation at all at first sight, as in vertebrates. But certain structural characteristics make it possible for this segmentation to be identified, and in particular is the distribution of cranial nerves important in this respect. This aspect of segmentation is dealt with more fully in Chapter XXIII. In fact, segmentation in any part of the body of a vertebrate is far from obvious, though it is apparent as regards the division of the vertebral column into separate vertebræ, and to some extent of the muscles into segmental blocks, as well as in the arrangement of the spinal nerves.

The Annelida. Members of this phylum may be distinguished by certain clearly-defined characteristics. They are segmented and cœlomate—i.e. they possess a cœlom. At the anterior end is an unsegmented prostomium, and often posteriorly there is an unsegmented pygidium, as in *Nereis*. The zone of growth is posterior, lying just in front of the pygidium, where this exists. Thus the oldest part of the animal is at the front end. They are all covered with a cuticle, which is secreted by the epidermis. Chætæ are usually present. Since the surface is cuticularised, locomotion is typically muscular, and not ciliary. The nervous system is of a distinctive type, consisting of a " brain " situated at the anterior a median **oviduct** opening on to the sternum of the eighth abdominal segment. Between the sterna of the eighth and ninth abdominal segments opens a **spermathecal pore,** within which the spermatheca bifurcates, but only one branch completes development, the other withering. On the ninth abdominal sternum are two openings from the pair of **collaterial glands,** which function to produce material for the formation of egg-cases. In the male a pair of **testes** occurs, and these organs are functional only in early life. From them spermatozoa are conveyed away along **sperm-ducts,** each of which becomes enlarged to form a **vesicula seminalis.** Each of these becomes so much subdivided that the two lying close together in the middle line are known as the **mushroom-shaped gland.** Here spermatozoa are stored throughout life and when required are passed along a muscular *ductus ejaculatorius,* into which both seminal vesicles discharge. This opens to the exterior by a median pore between the sterna of the ninth and tenth abdominal segments. Just ventral to this duct lies the **conglobate gland,** of doubtful function, opening confluent with the male genital pore. At copulation sperms are discharged into the spermatheca and later fertilisation occurs. Sixteen eggs are contained within each horny capsule and they undergo development in the genital pouch practically without sign of metamorphosis, so well marked in most insects. Concerned in the deposition of eggs are the gonapophyses in the region of the genital apertures. Morphologically these may represent modified abdominal appendages.

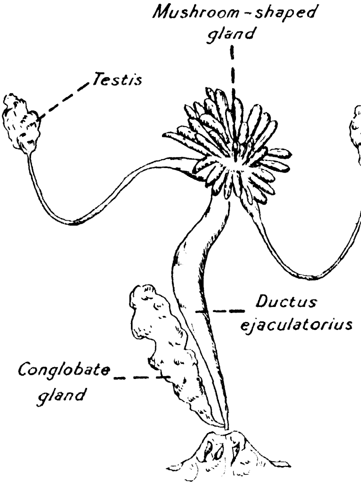


FIG. 41.—*Periplaneta.* Male reproductive system.

The Insecta. From the foregoing description the chief characteristics of an insect may be discovered. Thus it is an Arthropod with body divided into head, thorax and abdomen, the thorax consisting typically of three segments. It has three pairs of limbs and two pairs of wings, whilst breathing is effected by means of branched tracheæ. In common with other members of the phylum

Arthropoda it has jointed limbs and a hard exo-skeleton of chitin. Further, it has an open blood-vascular system, a very much restricted cœlom and a double, ventral nerve-cord enclosing the anterior end of the gut. The diagnostic features of the other classes of the Arthropoda will be considered later, but it is now necessary to discover the various ways in which this typical insect structure seen in the cockroach may become modified, and also to trace out the life-histories of a number of other insect types.

THE CABBAGE WHITE BUTTERFLY

External Features. In the description of this and succeeding types a knowledge of the structure of the cockroach will be assumed, and the characters of the types in question will be treated by comparison with this primitive form. Besides the pair of compound eyes found on the head there are, in addition, three simple eyes. The antennæ are clubbed at the tip, this character distinguishing between butterflies and moths. Most important is the modification of mouth parts, for these have become adapted to extracting nectar from the nectaries of various flowers. Accordingly, the maxillæ become closely apposed to each other to form a tube or proboscis through which the nectar may be drawn. When at rest it is coiled up to lie beneath the head. The remainder of the mouth parts are vestigial, only the hairy labial palps being developed to any appreciable extent. Each of the three segments of the thorax bears a pair of walking legs, whilst a pair of wings is found on both the meso- and the meta-thorax. These are large in proportion to the size of the slender body, and when at rest are held so that only the

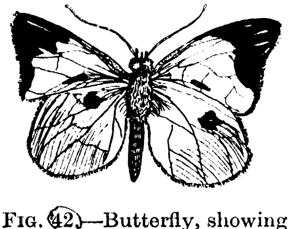


FIG. 42.—Butterfly, showing externals.

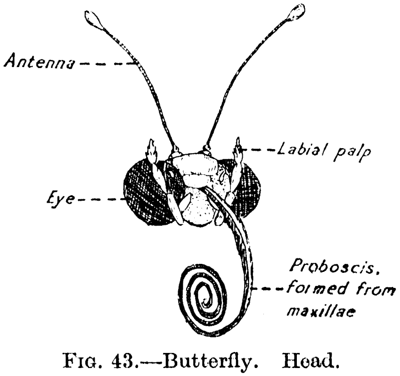


FIG. 43.—Butterfly. Head.

under surfaces are exposed. In this way a great many butterflies are protected by the concealment of the brilliant upper surface of their wings when at rest. The butterfly wing is covered with scales, these no doubt accounting for the curious iridescence as well as the bright coloration due to pigmentation. The presence of these scales accounts for the name Lepidoptera given to the order of insects to which the butterfly belongs.

Life-history. Egg-laying takes place normally at two seasons of the year, namely in late spring and late summer. The eggs are deposited in little masses of about fifty at a time on the under-surface of a cabbage or similar leaf, each egg being enclosed in a sculptured case. Development proceeds within this case, and after about ten days a small grub emerges, effecting its escape by means of its mandibles. Almost immediately it devours the egg-case, and this fact is not without significance for, once thus liberated, the caterpillar must attach itself by means of silk threads to the leaf of the food plant. This it does by secreting silk from a large **spinneret** on the front of the head. The silk in chemical composition is very like the material of which the egg-case is constructed, and thus the small grub can quickly produce this essential substance without its food having to undergo a complicated process of digestion and elaboration. At this point a feature common to all Arthropods must be mentioned. The animal is enclosed in a hard, chitinous exo-skeleton, and hence the degree to which growth can occur is severely limited. Accordingly, growth takes place in stages, and, prior to each, the old covering is shed. Increase in size takes place before the new coat becomes so hardened as to prevent it. This phenomenon of casting off the skeletal armour to facilitate growth is known as **ecdysis.** In the case of the caterpillar of the cabbage white butterfly three or four ecdyses occur before full size is reached. In this condition the animal is known as a **larva,** this being in the life-history of an animal a stage which leads an

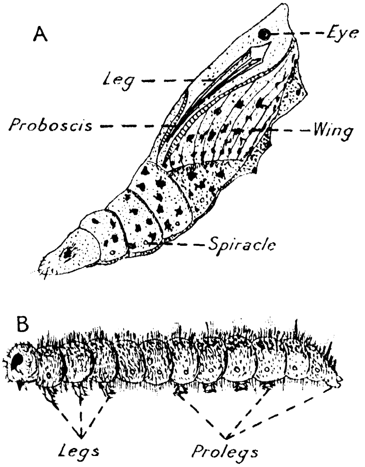


FIG. 44.—Development—stages in development.
A, Chrysalis. B, Caterpillar.

independent existence, but which differs in structure from the adult. The fully-formed caterpillar is of typical insect structure. It consists of a head, a thorax of three segments and an abdomen of ten segments. On each of the three thoracic segments is a pair of jointed legs, whilst on the third, fourth, fifth, sixth and tenth segments of the abdomen is a pair of **prolegs.** These are not true abdominal appendages, being merely outgrowths of the body-wall. This larva breathes by means of tracheal tubes, and on each of the first eight abdominal and the first thoracic segments there opens laterally a pair of spiracles (stigmata). On the head is a pair of large, toothed mandibles, five small simple eyes on each side, and a pair of very small antennæ, as well as the spinneret already mentioned. A pair of small maxillæ and a labium occur behind the mandibles. This larval stage is a voracious feeder, and at length it seeks a sheltered retreat where subsequent development may occur. It leaves the ground at this point and climbs some fence or tree, where it spins a pad of silk. This it grips with its hindermost pair of prolegs and then it winds a girdle of silk about the middle of its body to secure firm attachment. Some hours later the next stage, known as the **pupa,** emerges through a split along the dorsal side of the last larval skin. This shows in miniature the characters of the adult, for there may be identified three pairs of limbs, two pairs of wings, a pair of slender antennæ and a **proboscis.** These are at first free, but very soon they become closely applied along the body, which itself becomes much harder. Still attached to the silken pad this pupa now undergoes a resting stage, whilst within the pupal skin the structures of the adult insect are being shaped. This stage lasts for a varying length of time, for eggs laid in May become adults by August, whilst eggs laid in the late summer brood give rise to pupæ which survive in the quiescent state throughout the winter. Eventually the pupal skin splits along the dorsal surface and the adult or **imago** appears. This is at first soft and moist, but gradually it dries and the chitinous exo-skeleton becomes hardened, resulting in the perfected insect. This process whereby the larva becomes converted through the pupal stage to the imago is known as **metamorphosis.** As will be seen, therefore, metamorphosis is a well-marked series of changes resulting in a fundamental alteration in structure. In this case the biting and crawling caterpillar is converted into a sucking and flying butterfly. Another example will be found in Chapter XVIII, concerning the transformation of the larval tadpole to the adult frog. The sole function of the imago is the production of fertilised eggs, mating occurring on the wing.

THE HONEY BEE

This insect is of biological significance from several points of view, the first of which to be considered being its social habits.

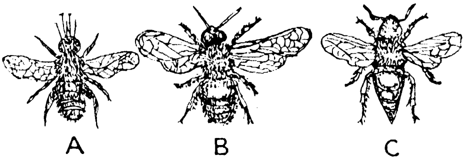


FIG. 45.—Honey bee. Members of hive.
A, Worker. B, Drone. C, Queen.

The members of a hive are functionally differentiated to a considerable extent. There is but one queen bee to a hive, and her purpose is the production of eggs. She is the only functional female, and in accordance with her habits there is found protruding from the tip of the abdomen a tube known as the **ovipositor,** concerned with the deposition of eggs. Connected with this tube is a duct from the poison gland, so that the same organ may be used also as a sting. The body of the queen is long and slender, which character distinguishes her from the workers whose abdomen is shorter. The workers are sterile females, and the ovipositor of the queen, as represented in the workers, functions exclusively as a sting. The edges of the structure are beset with backwardly projecting barbs, and in consequence the whole apparatus is frequently left in the flesh of the enemy, though the damage to the bee is usually fatal. The workers themselves are the smallest members of the hive, and their function is to collect nectar and pollen, as well as to construct the hive. Accordingly, their bodies show a number of distinct modifications. The legs and bodies of the workers are covered with hairs, so that pollen readily adheres to them. The hindermost pair of legs is further modified, for the outer surface of the tibia becomes concave to form a pollen basket or **corbiculum,** fringed by a number of large, curved

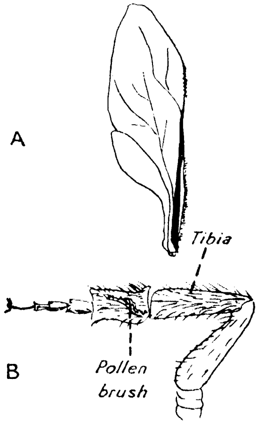


FIG. 46.—Honey bee.
A, Wing.
B, Hind leg.

hairs. The first tarsal joint on the same limb has likewise become very much enlarged, so that it can bear on its inner surface some nine rows of stiff bristles, forming the pollen brush. The pair of brushes functions to collect the pollen from the various parts of the body, and when full the hind legs are crossed and rubbed together so that the pollen becomes conveyed to the corbicula. In these vessels it is conveyed to the hive, where it is removed by a spine on the apex of the tibia of each of the middle pair of legs. Nectar obtained from flowers is converted into honey in the honey-stomach of the worker, corresponding to the crop of the cockroach. In order to remove the nectar from the nectaries of flowers it is essential that the mouth parts become modified to form a tubular structure. This is done in a manner quite different from that observed in the butterfly, so that, though the two proboscces function similarly, their morphological dissimilarity shows that they are independent evolutionary developments. The sucking tube of the proboscis of the honey bee is formed by the elongation and fusion in the middle line of the laciniæ of the labium, and is known as the **ligula.** It is enclosed in a sheath formed from the elongated maxillæ. Mandibles are well developed, and maxillary and labial palps are represented. Other modifications in the structure of the worker occur to facilitate the business of hive construction. On the ventral surface of the second to the fifth abdominal segments glands are found, concerned in the secretion of wax. This is produced in the form of plates, and in this condition is removed by spines on the first joint of the tarsus of each hind leg to be conveyed to the mandibles, where it is moulded into cells. It has been stated that the workers themselves are divisible into two groups, one (the cirières) concerned with the collection of provisions, and the other employed with the rearing of young. Alternatively it may be imagined that the latter function is undertaken by the younger workers which later in life become collectors. The honey-comb is worthy of note in that it

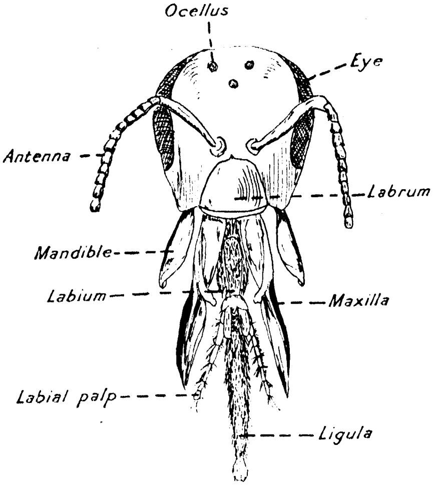
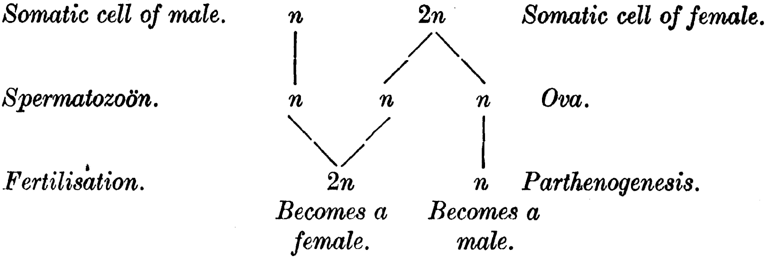


FIG. 47.—Honey bee. Head.

is so constructed as to yield the maximum of space with the minimum expenditure of material. Thus the cells are hexagonal in shape and built in double series placed back to back. There are two types of cell, known respectively as honey-comb and brood-comb. When a honey-comb cell is full it is closed with a wax cap, whilst the brood-cells remain open so that the nurses may supply the developing grubs with food. The brood-cells differ in size amongst themselves, the smallest being occupied by worker grubs, the few largest by queen grubs and the intermediate ones by drone grubs. Finally there exist in a hive the drones. These are the males, and, as will be seen later, contribute nothing to the maintenance of the hive, though any one of them may function to fertilise a young queen at flight. A typical hive contains but one queen, some six to eight hundred drones, and fifteen to twenty thousand workers.

Life-history. The sole function of the queen is the laying of eggs, one being deposited in each brood-cell. The question now arises as to how this single, egg-laying female can give rise to eggs from which the three different forms of bee can be derived. Prior to her confinement within the hive a young queen is fertilised by a male. This only supply of spermatozoa is stored by her throughout life, and she is able to lay either fertilised or unfertilised eggs. These develop respectively into females and males (drones). Whether the fertilised eggs become queens or workers is determined by the food supplied to the newly-hatched grub. In all cases the grubs emerge from the egg-cases about three days after laying and the fertilised eggs develop into females, whilst the unfertilised eggs undergo a process of parthenogenesis (development not preceded by fertilisation) to give rise to males. All the grubs are treated similarly by the nurses for the first three days, being fed on their regurgitated food. Subsequently the male (drone) larvæ are fed on pollen and the worker larvæ on honey, whilst the queens are retained on a diet of regurgitated food, known in consequence as "royal jelly." This is said to contain vitamin E, the fertility vitamin (p. 290). The larvæ are thus fed for some five days, after which a store of appropriate food is put into the cells, each of which is closed by a porous cap. During this period a short, pupal stage is undergone within a cocoon of silk which the larva has spun about itself. In all, the workers take some twelve days from the cessation of feeding by the nurses to the appearance of the adult insect, the drones occupying a slightly longer and the queens a somewhat shorter time than this. Whenever a new queen is produced there are two alternatives open. Either the new and the old queen may fight to the death of one of them, or the old queen may leave the hive. On so doing she is followed by a large number of workers, this constituting a swarm. It takes off in a mass from the hive, and, if coming to rest in some convenient place, may be " taken "—i.e. shaken almost solid into a bag or sheet and re-hived. If this does not occur the swarm must choose a new home, usually in a hollow tree-trunk. Meanwhile the new queen leaves the hive on her " nuptial flight," followed by all the males. One of these eventually fertilises her and then dies. The spermatozoa are stored for as long as five years, this being a reasonable duration of life for a queen bee, whereas workers last for only some two months. With the advent of winter the drones are cast out of the hive, whilst the queen and workers survive on the store of honey. Thus the whole life-history of a single individual is much the same as that of a butterfly, the egg hatching into a larva which in turn becomes a pupa for a short period before being finally converted into the adult form.

In Chapter XIV reference is made to certain highly-important structures contained in every cell and called **chromosomes.** These are constant in number in the cells of any one species of animal, and therefore, since fertilisation is effected by the fusion of two cells, each of the fusing cells must contain only half the constant number of chromosomes, so that between them they restore the full number in the fertilised egg. It is at once apparent that in the bee there must be certain peculiarities in the chromosome-constitution of the male, for it is produced from an unfertilised egg. In consequence the cells of its body (somatic cells) should contain only half as many chromosomes as do the somatic cells of a female, though subsequent reduplication results in their number being restored to the diploid to a great extent. What is even more important is that the spermatozoa to which the males give rise contain the same number of chromosomes as do their somatic cells, the usual halving of the number in the formation of germ-cells being avoided. But an egg produced by a female does undergo this halving of chromosome number, so that it contains as many of these chromosomes as does a spermatozoön. Thus, when an egg is fertilised, the double (diploid) number is restored, and thus a female is formed, but when an unfertilised egg develops parthenogenetically it gives rise to an organism containing only the single (haploid) number of chromosomes, and this is a male. This behaviour of chromosomes in the production and development of germ-cells in the honey bee may best be made clear by means of the following figure, where n may be taken to be the single (haploid) number of chromosomes and $2n$ the double (diploid) number of chromosomes.



Before attempting to understand this curious behaviour of the chromosomes of the honey bee the student is advised to become thoroughly conversant with the significance of chromosomes in cell division and the maturation of germ-cells in cases where no such anomalies arise.

AN APHID

Aphis is a genus of insects and comprises the plant lice. Its members are parasitic on plants, to which they do considerable damage. The species are named according to the plant each infests. Thus *Aphis rosæ* is the common blight of rose trees, *Aphis fabæ* lives on the bean, *Aphis humuli* on the hop, *Aphis granaria* on cereals, whilst *Aphis lanigera* is injurious to apple trees. In structure they are essentially similar to one another, and the following description may be taken to apply to any member of the genus.

External Features. These forms show the typical tripartite division of the body, the abdomen being shortened and fattened.

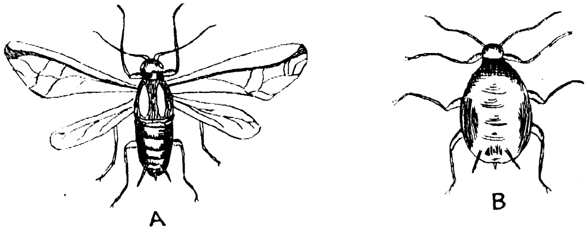


FIG. 48.—*Aphis*.
A, Winged. B, Wingless.

From the hind end of this region projects a pair of horny tubes, from which a sugary liquid, known as honey-dew, is said to be exuded. It seems more likely that it is discharged from the anus. It is a favourite food of ants. On the thorax may be found in some forms two pairs of erect wings, whilst other members of the same species are wingless. But it is in the head region that chief modifications have occurred, for the mouth parts are adapted to piercing and suctorial functions. The mandibles and maxillæ are modified to form four structures known as **stylets.** The inner two, formed from the maxillæ, become closely applied to each other except for two canals, known respectively as the **suction canal** and the **ejection canal.** These stylets are contained in a grooved **rostrum,** representing the labium, which has become sheath-like in form. The labial and maxillary palps are atrophied. The stylets are used for piercing the host plant, when saliva is pumped into the wounded tissues along the ejection canal and the liquid contents of the plant

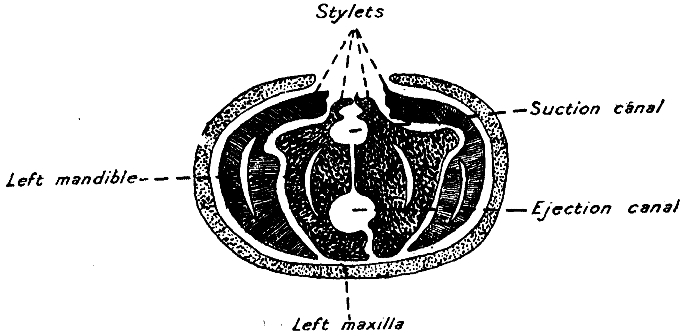
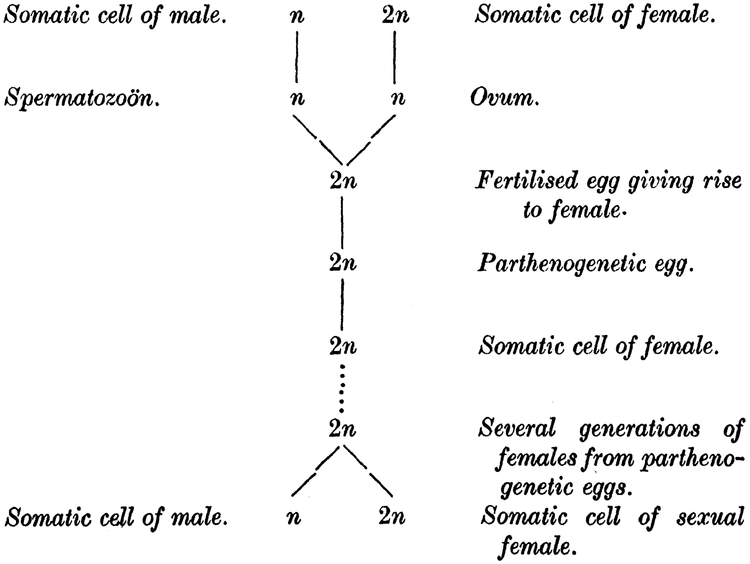


FIG. 49.—*Aphis.* Section of rostrum.

absorbed through the suction canal. Thus these aphids may cause plant diseases partly by their own deleterious effect on the tissues, and partly by their facilitating the entry into the plant of bacterial and fungoid spores through the wounds which they inflict. On the head is a number of ocelli, as well as the usual pair of compound eyes.

Life-history. This is of interest on account of the fact that again parthenogenesis occurs as well as ordinary sexual reproduction, the two processes being seasonal in appearance. Thus in the autumn males and perfect females are formed. These females lay fertilised eggs, and either the eggs themselves or pupæ developed from them are capable of surviving the winter. Eventually in the following spring they give rise to females which reproduce parthenogenetically to form further females. These reproduce in a similar manner, and so, during the summer, a large number of generations of parthenogenetic females is produced, thus ensuring rapid multiplication. It is interesting to note that these forms bring forth their young alive, and are therefore described as viviparous. In the autumn males and perfect females are produced, so that it must be assumed that change in weather conditions is responsible for the different products now developed from the parthenogenetic eggs. Thus here is another example of alternation of generations, sexual reproduction taking place in the autumn to produce forms capable of surviving the winter, whilst in the spring and summer rapid, parthenogenetic development of eggs ensures enormous multiplication. These imperfect females, as well as the males, are usually winged, whilst the females laying the fertilised eggs are wingless.

The chromosomal behaviour in the various generations of aphids and their germ-cells is of importance. The sexual female (i.e. the one laying the fertilised eggs) contains the double (diploid) number of chromosomes in her somatic cells, whilst this becomes reduced to the haploid in every egg to which she gives rise. The males, on the other hand, contain only the haploid number in their somatic cells, so that no reduction occurs at the formation of spermatozoa. Thus when an egg is fertilised by a sperm the diploid number of chromosomes is restored. This gives rise, therefore, to a female. Now this produces eggs with no reduction in chromosome number, so that they develop parthenogenetically within the body to give rise to more females, all with the diploid number of chromosomes in their somatic cells and in their ova. But eventually, presumably


Somatic cell of male.
n
2n
Somatic cell of female.
Spermatozoön.
n
n
Ovum.
2n
Fertilised egg giving rise to female.
2n
Parthenogenetic egg.
2n
Somatic cell of female.
2n
Several generations of females from parthenogenetic eggs.
Somatic cell of male.
n
2n
Somatic cell of sexual female.

This cycle is repeated once annually.

as a result of the stimulus of changed weather conditions, some of these eggs do undergo a reduction of chromosome number to the haploid state, and therefore, though they develop parthenogenetically, they give rise to males. Other eggs at this same time, though not undergoing a reduction of number of chromosomes, give rise to females with perfectly-formed reproductive organs. These are the sexual females, and the eggs to which they give rise will only proceed with development if they are fertilised. This behaviour of the chromosomes may be summarised as shown on page 69, where n is taken to be the haploid number of chromosomes and $2n$ the diploid.

The Insecta. In conclusion of the study of the Insecta it may be well to notice the diagnostic features of a few of the more important orders into which this enormous class is subdivided. The order Orthoptera has been well exemplified by the cockroach, the Lepidoptera by the butterfly, the Hymenoptera by the honey bee, and the Hemiptera by *Aphis*, so that nothing further need be added to these. Amongst others may be mentioned the order Coleoptera, including the beetles. These have biting mouth parts and the fore-wings are in the form of shields covering the hind ones. These insects are distinguished from members of the order Orthoptera, however, by the fact that metamorphosis is complete. The order Anoplura includes the lice. They are all ecto-parasitic on birds and mammals, wingless, and with eyes very much reduced or entirely absent. In accordance with their habits the mouth parts are highly specialised. So specific are the bird lice in the particular type of bird they infest that in some cases the relations between different birds have been traced by reason of the fact that they carry the same species of Mallophaga (bird lice).

The Arthropoda. The Insecta is only one of the classes into which the phylum Arthropoda is divided. The members of this phylum are bilaterally symmetrical, metamerically segmented Triploblastica, whose bodies are enclosed in a chitinous exo-skeleton. The blood-vascular system is open, whilst the cœlom is practically confined to the cavities of the gonads. Each segment primitively bears a pair of jointed appendages, which become variously modified and in many cases disappear completely from some regions. The class Insecta has already been dealt with, and the class Crustacea is exemplified by the crayfish, described in Chapter IX. The class Myriapoda is comprised of centipedes and millipedes. Being terrestrial forms they breathe by means of tracheæ. They have numerous pairs of legs and are further characterised by the absence of wings. The only other class of consequence for present purposes is the Arachnida, this including the spiders and scorpions. The body of the spider is divisible into two regions only, the **cephalo-**

thorax or prosoma and the abdomen, separated by a waist and each covered with a shield. All traces of segmentation become obscure and at the anterior end are two central and six lateral eyes. These are borne on an unsegmented prostomium, whilst at the hind end of the animal is an unsegmented pygidium. The Arachnida have typically twenty segments between the prostomium and the pygidium. There are no antennæ, which means that the first segment is without appendages. The first pair of limbs is found on the second segment. They are known as **cheliceræ,** and are in connexion with the poison gland. The third segment bears a pair of small appendages known as **pedipalps,** which are of sensory function. The pedipalps of the mature male are modified to form a copulatory organ for the transference of spermatozoa. There are four pairs of walking limbs, one on each of the four segments immediately succeeding the pedipalps, and they end in bifid claws. On the first abdominal segment is found a genital operculum and a pair of **lung-books.** These are nothing more than cavities opening to the exterior on the ventral surface and containing a number of highly-vascularised projections of the body-wall. These may occur also on the second abdominal segment. The third and fourth abdominal segments each bear short, paired appendages, known as **spinnerets** and used for the construction of webs. They are regarded as reduced and modified limbs. The internal anatomy is a modified version of that of the cockroach. The heart is in the abdominal region, whilst all the ganglia of the nervous system are coalesced into an œsophageal ring, from which nerves emerge to peripheral parts. The cœlom is represented in coxal glands at the base of each walking leg, as well as in the cavities of the gonads. The sexes are separate, and sexual dimorphism is a common feature amongst spiders. The males are frequently so much smaller than the females that they are devoured by their mates subsequent to copulation. Development takes place within a cocoon of silk and there is no metamorphosis or larval stage.

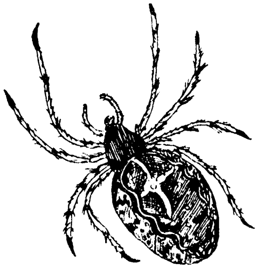


FIG. 50.—Garden spider.

CHAPTER IX

ASTACUS. PARASITIC CASTRATION

Astacus (the crayfish) is an Arthropod belonging to the class Crustacea. Members of this class are distinguished by the presence of two pairs of antennæ and, since the majority of them are aquatic, the possession of gills for respiratory purposes. The English species, known as *Astacus torrentium,* is found in rivers, where it makes small burrows in the banks.

External Features. Being an Arthropod it is enclosed in a continuous exo-skeleton of chitin, calcified in places to form a number of plates. The whole body is segmented and each segment bears a pair of appendages. This must be regarded as the primitive condition amongst Arthropods. At the anterior end the calcified plates have become fused to form a large cephalothoracic shield or **carapace.** There is an anterior, unsegmented prostomium, separated by twenty segments from a posterior, unsegmented pygidium, known in the crayfish as the **telson.** This telson is divided by an imperfect transverse joint, and beneath it lies the anus. At its anterior end the cephalothoracic shield is extended forwards to form a **rostrum,** whilst a transverse **cervical groove** denotes the line of separation between the head and the thorax. In the abdominal region, situated between the cephalothorax and the telson, the segmental plates are separate. Each is composed of a dorsal tergum and a ventral sternum, joined on each side by a V-shaped **pleuron** in all save the first abdominal segments. The part of the sternum between the point of attachment of a limb and

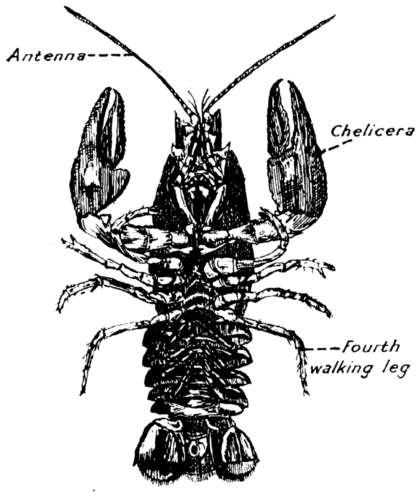


FIG. 51.—*Astacus.* Ventral view.

the pleuron is known as the **epimeron.** The terga overlap to some extent, and the limbs are attached near the postero-lateral corners of the sterna. On each side the carapace is expanded laterally into an overhanging fold, known as the **branchiostegite** or gill-cover, which forms the margin of a cavity containing the gills. The branchiostegite is demarcated from a median, cardiac region by a **branchiocardiac groove** on either side. At the anterior end is the mouth, opening on to the ventral surface between the third and fourth segments, whilst at the sides of the rostrum are the eyes, set on a pair of short stalks. These stalks are probably not true appendages, but they belong to the first segment of the body, and

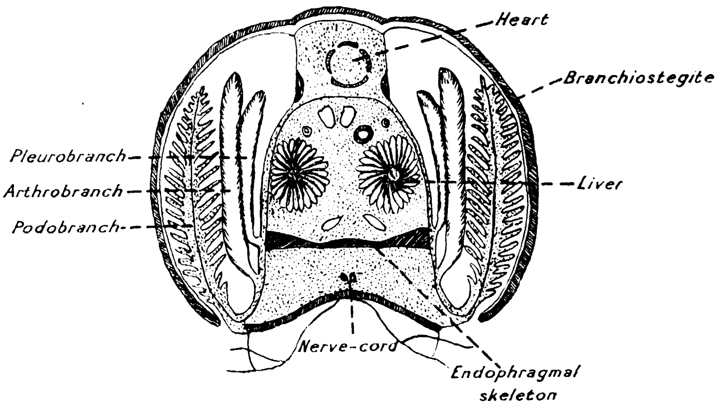


FIG. 52.—*Astacus.* Transverse section.

no other structures are borne on it. It is the appendages of the crayfish which are of chief importance, for they show various types of modification from the primitive condition. It is only in the abdominal region that any approximation is made to a typical Arthropod limb. Each limb is attached to the body by an arthrodial membrane. In accordance with the backward movement of the mouth to lie between the third and fourth segments fused portions of the skeletal armour of the first three segments form a labrum (upper lip) in front of the mouth and a labium (lower lip) behind the mouth.

Appendages. There are, in all, nineteen pairs of appendages, the eye-stalks borne on the first segment not being so regarded. An appendage consists typically of a basal region, known as a **protopodite** and subdivided into a proximal **coxopodite** and a distal **basipodite.** This protopodite bears on its inner side an **endopodite** and on its outer side an **exopodite.** The endopodite may be five-jointed, the joints being then known as ischiopodite (proximal),

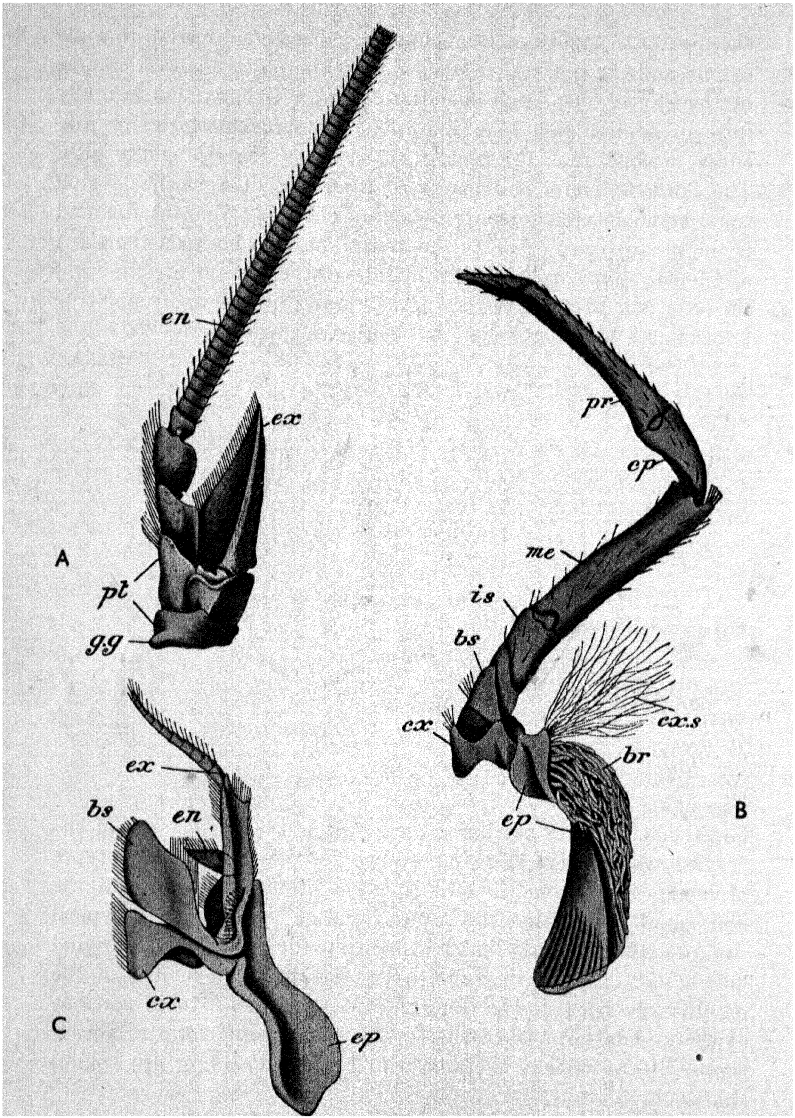


FIG. 53.—*Astacus.* Appendages.
(From " Atlas of Practical Elementary Zootomy," by G. B. Howes.)
Key is below, Fig. 54.

meropodite, carpopodite, propodite and dactylopodite. The various appendages will now be considered in turn and their chief characteristics noted. The description will be begun from the hind end of the animal, since in this region the limbs are less specialised.

(*a*) *Abdominal Appendages*. These are found on segments 15 to 20. Those of segment 20 are somewhat modified in that the endopodite and exopodite have become broadened. They combine with the telson to form the tail-fan. Those on segments 19 to 17 are typical, with the endopodites slightly longer than the exopodites and both beset with numerous bristles. They tend to be larger in the female than in the male. The appendages of segment 16 are typical in the female, but in the male are considerably enlarged and turned permanently forwards. The base of the endopodite of each

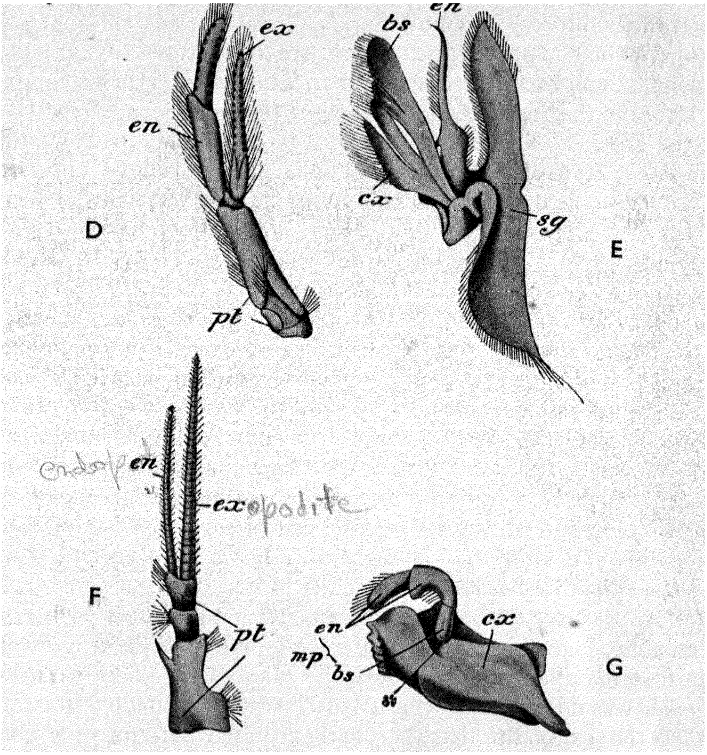


FIG. 54.—*Astacus*. Appendages. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.) A, Antenna. B, Penultimate ambulatory appendage. C, First maxilliped. D, Third abdominal appendage. E, Second maxilla. F, Antennule. G, Mandible.

br, gill (podobranch); *bs*, basipodite; *cp*, carpopodite; *cx*, coxopodite; *cx.s*, coxopoditic setæ; *dc*, dactylopodite; *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *is*, ischiopodite; *me*, meropodite; *pr*, propodite; *pt*, protopodite.

limb is hollowed out and curved over to form a tube, which serves as a copulatory organ. The first abdominal appendage (segment 15) has no exopodite in either sex, and in the female it is vestigial or entirely absent. In the male the basipodite and endopodite are fused, the resultant structure being curved and hollowed out to assist in the process of copulation.

(*b*) *Thoracic Appendages.* These are constituted by a pair of appendages on each of segments 14 to 7 inclusive. On segments 14 to 10 occur the walking legs. Each of these limbs is characterised by the absence of an exopodite, whilst the endopodite is long and composed of five segments named as in the typical appendage already described. Each of the appendages of segment 14 has its coxopodite pierced by a small male pore. Each of the legs on segments 13 to 11 bears on its outer side a thin-walled extension, known as an **epipodite,** from which a number of filamentous processes project to form a gill. On each of the appendages of segment 12 in the female a genital pore is borne on the coxopodite. Segment 10 bears a pair of large **chelipeds,** very like the walking legs in structure, but distinguishable from them by their size and by the fact that the dactylopodite (the distal joint of the endopodite) is modified to form pincers. Segments 9 to 7 bear appendages known as **maxillipeds.** Each is a fully-developed limb in that all the parts are represented, but whilst the maxillipeds of segments 9 and 8 bear epipodites and gills, that of segment 7 has a reduced endopodite, and the epipodite has no gill attached to it.

(*c*) *Appendages of the Head.* Segments 6 and 5 bear each a pair of **maxillæ,** known as the second and the first maxillæ respectively. The first maxillæ are also called the maxillules. The endopodite of each second maxilla is a narrow structure directed forwards, whilst the exopodite has become expanded into a wide plate, situated at the front end of the branchial chamber and known as the **scaphognathite.** It functions to maintain a current of water in the gill-chamber. The first maxillæ are smaller in size and the exopodite is not represented. On segment 4 occurs a pair of **mandibles.** Each is very much hardened and provided with tooth-like processes biting on those of the other member of the pair. The stout portion of the mandible is the coxopodite, which bears a small, three-jointed palp composed of basipodite and endopodite. Segments 3 and 2 bear the **second** and **first antennæ** respectively. Each second antenna consists of a short, broad coxopodite, on the base of which opens the green gland (excretory organ). It has a small endopodite bearing a many-jointed "feeler." On segment 2 occurs a pair of first antennæ (antennules). It is peculiar in so far as its protopodite is divisible into three, instead of the usual two, portions, whilst a pair of processes emerging from this are usually regarded as the endopodite and the exopodite respectively. At the base of this organ opens a statocyst, described later in the present chapter. The following table may assist in understanding the chief features of the various appendages of the crayfish. The study of appendages is best begun from the hind end, since in this region they are more typical.

Segment	Appendage	Chief Characteristics	Function
20	Abdominal limb	Endopodite and exopodite broad	Tail fan
19–17	Abdominal limbs	Typical. Larger in the female	Paddles
16	Abdominal limb	Typical in female. Endopodite of male assists in copulation	Paddle
15	Abdominal limb	Vestigial or absent in female. Endopodite of male assists in copulation. No exopodite	Copulation
14	Walking leg	Large endopodite. No exopodite. Male genital pore.	Walking
13	Walking leg	Large endopodite. No exopodite. Epipodite with a gill	Walking
12	Walking leg	As 13, but with female genital pore	Walking
11	Walking leg	As 13	Walking
10	Cheliped	As 13, but larger	Capture of prey
9–8	Maxillipeds	Large endopodite. Epipodite with gill	Jaws
7	Maxilliped	As 9, but epipodite without gill	Jaws
6	2nd maxilla	Exopodite is scaphognathite	Jaws
5	1st maxilla	No exopodite	Jaws
4	Mandible	Thickened and hardened coxopodite with palp from basipodite and endopodite	Jaws
3	2nd antenna	Endopodite bears " feeler." Green gland opens at base	Sensory organ
2	1st antenna	Protopodite of three portions. Statocyst at base	Sensory organ

Segments 20 to 15 (inclusive) comprise the abdomen, segments 14 to 7 the thorax and segments 6 to 1 the head.

Respiratory System. This system will be dealt with now, since the structures which comprise it are external gills and are therefore of importance in a consideration of the external features. Gills are branched, thin-walled structures borne in various positions within the gill-chambers. Blood is circulated in them so that gaseous exchange can be effected, the blood absorbing the dissolved oxygen of the water, into which its waste carbon dioxide escapes by diffusion. The water is kept in motion in each gill-chamber by the beating movements of the scaphognathite of that side, formed from the exopodite of the second maxilla. The water is driven forwards from beneath the branchiostegite, and in its escape it flows near the opening of the green gland on the second antenna, thus carrying away the waste products discharged by this excretory organ. The gills themselves are named according to their position of attachment. Thus, those arising from the epipodites of the limbs are known as **podobranchiæ.** Others arise either from the arthrodial membranes or from the inner wall of the gill-chamber, and are known respectively as the **arthrobranchiæ** and the **pleurobranchiæ.** The positions of these various types of gill are important. Podobranchiæ occur on all the thoracic limbs except the first (1st maxillipeds) and the last (last walking legs). The first maxilliped bears an epipodite, but no gill. Two arthrobranchiæ—an anterior and a posterior—are also found on each limb bearing a podobranchia, except in the case of the second maxilliped which bears only an anterior arthrobranchia. There is only one pair of pleurobranchiæ, borne one above each of the last pair of thoracic appendages (walking legs). Above the three pairs of limbs preceding this are vestigial pleurobranchiæ. The following table will serve to show the relationships between the positions of the various types of gill.

Let *aa* = anterior arthrobranchiæ, *pa* = posterior arthrobranchiæ, *p* = podobranchiæ, *pl* = pleurobranchiæ, and *v* = vestigial gill.

Segment	7	8	9	10	11	12	13	14
	Epip.	*p* *aa*	*p* *aa* *pa*	*p* *aa* *pa*	*p* *aa* *pa* *v*	*p* *aa* *pa* *v*	*p* *aa* *pa* *v*	*p* *pl*

Alimentary System. Of the various internal organs of the crayfish only those comprising the nervous system will be dealt with in detail, whilst the remainder will be reviewed in outline. As in the cockroach the body-cavity is a spacious hæmocœl. From the mouth the food passes through a wide œsophagus into the gizzard, known also as the **proventriculus** or gastric mill. This is divided into an anterior, cardiac region, known as the mill chamber, and a posterior, pyloric region, known as the filter chamber. In the former the food is masticated, whilst large particles are prevented from passing through the latter by a system of processes forming a strainer. The part of the gut so far described is a stomodæum, i.e. it is of ectodermal origin. Now follows the true endodermal portion of the gut, termed the mesenteron, from which a pair of branched liver diverticula, of digestive function, are given off. The gut ends in the form of an ectodermal intestine (proctodæum), where absorption takes place despite the presence of a chitinous lining.

Vascular System. The heart lies in the centre of the dorsal region of the body. It is a median, muscular sac, opening by three pairs of ostia, each of which is guarded by a valve, into the surrounding pericardial space which, being hæmocœlic, is filled with blood. Blood is conveyed away from the heart by six arteries which soon become considerably subdivided, but no proper capillary system is present. Instead the blood flows into large spaces, which unite to form sinuses. From the largest of these sinuses—the perivisceral—the blood is conveyed to the gills. After oxygenation here it is returned to the pericardial space and so back to the heart. The heart is held in position by six muscular bands—alæ cordis—attached to the wall of the pericardial chamber. The blood itself contains leucocytes, whilst the respiratory pigment is a copper compound known as hæmocyanin, borne in the plasma and not in special corpuscles.

Excretory System. This consists of a pair of closed cœlomic sacs, known as end sacs, from each of which issues a coiled duct to open at the base of the second antenna after first expanding to form a thin-walled bladder.

Nervous System. This is constructed on the same plan as in the Annelida. At the anterior end is a **supra-œsophageal ganglion,** from which nerves emerge to supply the sensory structures of the first three segments. From this ganglion arise two **circumœsophageal commissures** to unite in the **subœsophageal ganglion,** nerves from which supply the appendages as far back as the eighth segment (inclusive). Here, therefore, ganglia have become considerably coalesced, signifying that the process of cephalisation has taken place to a great extent. Passing posteriorly from this subœsophageal ganglion is a ventral nerve-cord, distinctly double in the thoracic region, whilst in the abdomen the two component cords have become fused together. In each thoracic segment there is, therefore, a pair of ganglia, whilst in the abdomen each ganglion appears to be a single structure, though of double origin. The gut is supplied by a visceral nerve from the supra-œsophageal ganglion.

The sense organs of the crayfish consist of a pair of compound eyes and a pair of statocysts. The eyes are similar to those of the cockroach, described on page 58. Each statocyst is a hollow sac at the base of the first antenna. Being an ectodermal invagination it is lined with chitin and bears a large number of sensory hairs or setæ. Contained in the cavity are grains of sand (**statoliths**) in contact with the sensory setæ. The function of these organs is that of orientation, equilibrium being established when the statoliths fall evenly on the central setæ and not to excess on those of any one side. It has also been suggested that they may be able to appreciate vibrations. At every ecdysis the lining of the statocysts is shed, so that the statoliths are lost and must be replaced by new ones. This fact was made use of in the closely-related prawn to test the efficacy of these statocysts as organs of balance. Accordingly, instead of sand, finely divided iron was introduced into the water, and was made use of by the animals to function as statoliths. It was then discovered that the prawns could be made to vary their position of orientation by moving a bar magnet from place to place around them.

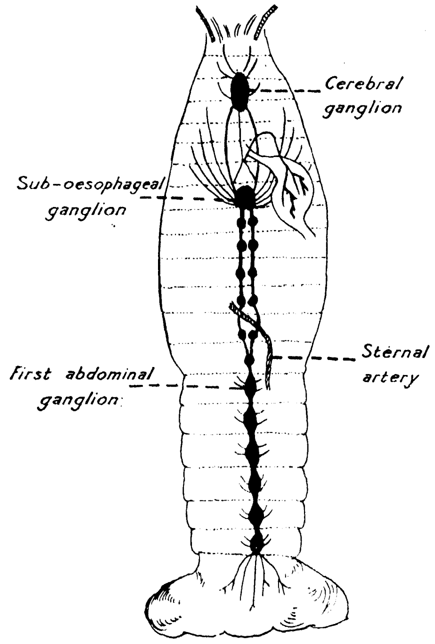


FIG. 55.—*Astacus* Nervous system.

Reproductive System. The sexes are separate, as already discovered when studying the external features. The genital organs are simple and fundamentally similar in both sexes. The ovaries consist of three sacs discharging into a pair of oviducts which open to the exterior on the bases of the limbs of segment 12. The testes are similarly trilobed, each of the pair of ducts (vasa deferentia) becoming much coiled before opening on to the coxopodite of the last walking leg (segment 14). Pairing takes place in autumn, when copulation is effected by the male passing a packet of spermatozoa on to the under surface of the female near the openings of the oviducts. A spermatozoön consists of a small, nucleate mass of protoplasm from which a number of stiff processes emanate. Several such are cemented into a packet by means of a secretion produced by the walls of the vasa deferentia. Eggs are not laid till some month later, and fertilisation is effected by the entry of a single sperm into an egg, early development taking place while the embryo is still attached to the mother.

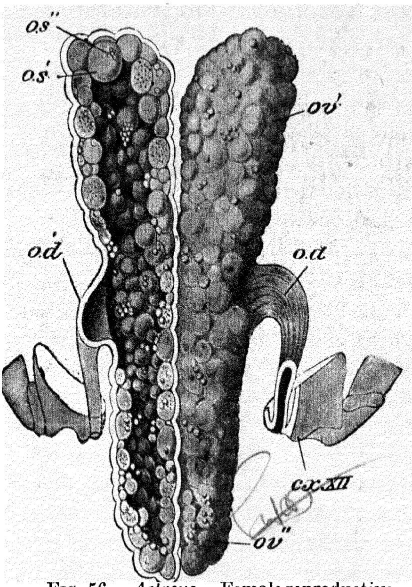


Fig. 56.—*Astacus.* Female reproductive organ. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

o.d, right oviduct; *o.d'*, left oviduct; *o.s'*, ripe ovisac; *o.s''*, immature ovisac; *ov'*, anterior paired lobe of ovary; *ov''*, median lobe; *cx.XII*, coxopodite of antepenultimate ambulatory appendage.

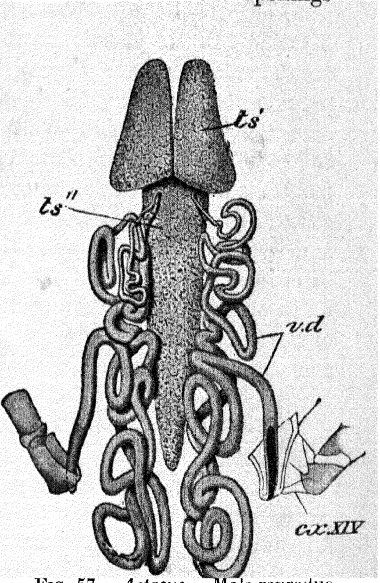


Fig. 57.—*Astacus.* Male reproductive organs. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

ts', testis (paired lobe); *ts''*, testis (median lobe); *v.d*, vas deferens; *cx.XIV*, coxopodite of last ambulatory appendage.

Cuticular Skeleton of Arthropods. One of the chief characteristics of the phylum Arthropoda is the presence of a chitinous exoskeleton. Some consideration must therefore be devoted to it.

Chitin is secreted by cells of the epidermis, so that the outer layers are the oldest. In view of this continuous, chitinous covering there are no gland cells in the epidermis. Yet the surface of the animal is in many places highly sensitive. This is effected by means of a number of pits in the cuticle, each ending in a sensory seta, into which a nerve fibre projects. Some of the setæ are of purely mechanical function, however. The whole chitinous cuticle not only acts as mere armour, but also protects the animal from invasion by ecto-parasites. It further functions to give rigidity, for the epidermal cells beneath it are observed frequently to bear processes to which muscles are attached. Cilia are characteristically absent from the Arthropoda. The shedding of the old, chitinous covering, constituting the process of ecdysis, has already been mentioned. When this occurs it is noted that large quantities of gastroliths (small, calcareous bodies) occur in the proventriculus, and they are used up in the calcification of the new cuticle. Prior to ecdysis the tissues become loaded with glycogen, which is used up in bringing about the rapid change in size before the hardening of the next skeleton. At ecdysis the chitin lining the stomodæum and proctodæum is shed, as well as that of the general body-surface.

PARASITIC CASTRATION

Before leaving the Arthropoda mention must be made of the phenomenon which, so far as is known, is confined exclusively to a few members of this phylum. In all fully-investigated cases the sex of an animal is found to be determined by the genotypic constitution[1] of that organism, and there is no reason to believe that this is not true universally throughout the animal kingdom, whereever the phenomenon of sex is found. The degree of determination exercised by the genotype varies in different groups of animals. Thus in Insecta it is an insuperable force, and should any cell in the early stages of an embryo, by some mitotic catastrophe, come to be the sexual opposite of the remainder of the cells, this difference will be perpetuated in all future generations of cells derived from this "freak," and a gynandromorph will result, in which the characters of both sexes co-exist entirely independently. Excision and inplantation of gonads—admittedly difficult tasks—are believed to have no positive effects on the sex characters of insects. In birds and mammals the action of the gonads in determining the sex characters of the remainder of the soma is profound, so much so that sex determination in these classes is said to be of the following order. A bird (or mammal) develops an ovary or testis according to whether its genotypic constitution is male or female : the sexual properties of the soma depend on the type of gonad produced—male features accompany the development of testes, and female features that of ovaries. Thus gonadectomy and transplantation in birds and mammals widely affect the constitution of the soma. The phenomenon of parasitic castration has been noted amongst certain insects, but is chiefly found in the Crustacea, and it must be stated that, so far as is known, the gonads bear but little relation to the development of various sexual attributes in this class, which does, in fact, closely resemble the Insecta in that the constitution of every cell is determined by its particular genotype.

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[1] See the author's "Inheritance and Evolution" (Methuen, 1936) for the genetics of sex determination.

Parasitic castration may best be understood by means of examples, after which explanations will be advanced. *Upogebia littoralis* (a Crustacean belonging to the same order as does the crayfish) is usually found to be parasitised by *Gyge branchialis*, itself a small Crustacean. To some extent this parasite modifies the structure of both sexes of *Upogebia* equally, but in respect of certain appendages, which, since they are of importance in reproduction may be regarded as secondary sexual characters, there occurs a distinct feminisation. For instance, the first pair of abdominal appendages are developed normally only in the female, where they appear seasonally to receive sperm-packets (spermatophores) and to carry the eggs. Their growth is slightly retarded in the parasitised female, but in the parasitised male they are developed almost to perfection. In the parasitised female the ovaries almost always atrophy to such an extent that breeding is impossible, whereas in the parasitised male testes may have degenerated but slightly, if at all. The course of parasitisation is interesting. In the swollen branchiostegite (gill-chamber) of *Upogebia* live a male and female *Gyge* as ecto-parasites. The fertilised eggs which they produce grow each into a microniscus larva, which itself becomes temporarily parasitic on a pelagic crustacean. Soon it becomes liberated to form a crytoniscus larva, with well-developed chitin, limbs and muscles. Finally this invades the very young stage of a *Upogebia*, the first parasite so to do becoming a female, whilst the next larva to enter the host settles down on the female already present and develops into a male.

A further example of parasitic castration is that of *Inachus* (a crab) by *Sacculina*. Here again the male has undergone a distinct feminisation in respect of secondary sexual characters. The parasite itself may be regarded as internal, for from it extend suckers to penetrate nearly all the tissues of the host, avoiding, however, the vital organs. This is a remarkable adaptation, for, should the parasite injure the vital organs of the host, it would effect its own destruction and prejudice the perpetuation of the stock.

A few instances of parasitic castration are known amongst insects, including the Hymenoptera. The solitary bees and wasps may be parasitised by *Stylops* or *Xenos*, themselves insects of the order Strepsiptera. The female is larviform and never leaves the body of the host, whilst the male is winged in adaptation to distribution. Eggs are fertilised through a tube projecting from the body of the female, and fertilised eggs are then deposited on flowers visited by the infected insects, so that fresh contamination is thus effected. As a result of this parasitisation feminisation of the male Hymenopteran may occur.

In explanation of this phenomenon it has been suggested that the parasite may well be the physiological equivalent of an ovary. Thus it will come about that the male will show such female characteristics as depend for their development in that sex on the presence of an ovary. The gonads appear to control the development of secondary sexual characters in Crustacea and insects not by means of any hormonic secretion, but by their action as physiological units, more in the manner in which the same process is effected in birds. The completeness of the feminisation in the case of *Upogebia* is explicable on the grounds of the early invasion by the parasite, whilst in *Inachus* this invasion can occur at any period in the life of the host. Once fully developed the structures cannot so readily be modified. The partial destruction of the ovary in the female *Upogebia* is no doubt due to its being robbed of nourishment, for its normal supply must be very much greater than that of a testis, which undergoes little or no change during parasitisation.

of secretory and absorptive function. It communicates with the stomach by several ducts. Leading from the lower part of the stomach is a coiled intestine, which later gives place to a straight rectum. This structure is actually situated in the pericardium and surrounded by the ventricle. Further, its dorsal wall has become invaginated to form a **typhlosole,** which assists in absorption. From the right side of the stomach projects a blind outpushing, known as the **cæcum,** in which a structure called a **crystalline style** makes seasonal appearances. It is a gelatinous rod of protein material, functioning as a reserve supply of food.

Body-cavity. The body-cavity of *Anodonta* is partly cœlomic and partly hæmocœlic. The pericardial cœlom encloses the heart and rectum, and communicates with the exterior by a pair of excretory tubes. The cavities of the gonads also are cœlomic. Since the blood-circulation of the mussel is open the remainder of the organs are contained in an hæmocœl.

Vascular System. The heart lies in the pericardium and consists of an anterior ventricle, which receives blood from two small, posterior auricles. The ventricle may be regarded as comparable to the dorsal blood-vessel in the Annelida and Arthropoda, having become extended ventrally on either side of the rectum in the mussel, finally to enclose it. Blood from the ventricle passes forwards along an anterior and backwards along a posterior aorta for distribution, finally reaching the hæmocœl. Before it is returned to the auricles it is circulated through the kidneys for purification and through the gills for oxygenation.

Respiratory System. The arrangement of the gills in *Anodonta* is both interesting and important. As has been pointed out, there are two gills on either side of the body, and each consists of two **lamellæ,** continuous ventrally so that each gill is V-shaped in transverse section. The line of junction between each gill and the ventral surface of the body is known as the **axis.** It can be assumed that primitively each gill was a single lamella, but that during evolution it has become elongated and bent backwards towards the dorsal surface, the free end of the outer lamella of the outer gill fusing with the mantle and that of the inner lamella of the inner gill anteriorly with the foot. In this way each V-shaped gill comes to enclose a space, known as the **epibranchial space.** Farther back the edge of the inner lamella of the inner gill becomes freed from the foot, whilst still more posteriorly it joins the corresponding structure of the other side. In this latter region, furthermore, the axis of the gills has become liberated from the ventral surface of the body. Accordingly, at the anterior end there are found to be four distinct epibranchial spaces, whilst posteriorly these have

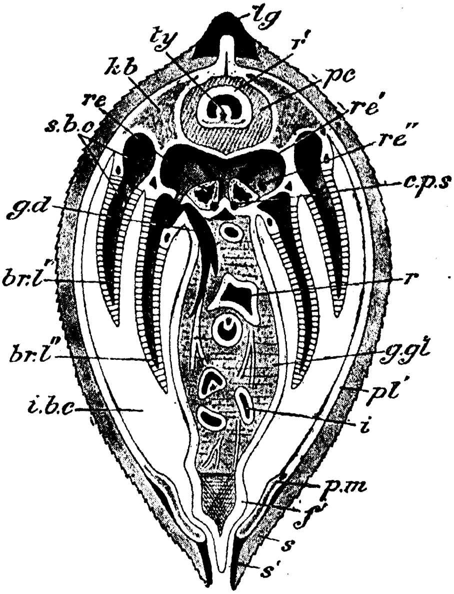


FIG. 59.—*Anodonta.* Transverse section of body. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

br.l′, left outer gill; *br.l″*, left inner gill; *c.p.s*, cerebro-visceral commissure; *f′*, muscular foot; *g.d*, genital duct; *g.gl*, gonad; *i*, intestine; *i.b.c*, infra-branchial chamber; *kb*, Keber's organ; *lg*, ligament; *pc*, pericardium; *pl′*, pallial lobe; *p.m*, pallial muscle; *r*, *r′*, rectum; *re*, kidney; *re′*, right renal sac (ureter), here confluent with its fellow; *re″*, reno-pericardial aperture; *s*, valve of shell; *s′*, shell, inturned free border; *s.b.c*, supra-branchial chamber; *ty*, typhlosole.

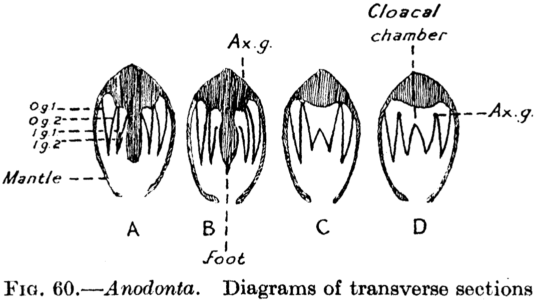


FIG. 60.—*Anodonta.* Diagrams of transverse sections, showing attachment of lamellæ of the gills.

coalesced to form a single **cloacal space,** from which water passes to the exterior through the exhalant siphon. Since the anus opens into this cloacal space the waste matter is carried away in the respiratory current. Each gill is composed of a number of very closely-applied, parallel filaments, fused at intervals along their inner edges and perforated so as to allow the entrance of water into the interlamellar space. Thus, water enters through the inhalant siphon at the posterior end into the mantle cavity. From here it passes through the apertures in the gill lamellæ into the interlamellar spaces and thus into the epibranchial spaces. By the beating movements of the cilia borne on the gills water is propelled through the cloacal space to the exterior. Since the kidneys discharge their contents into the inner epibranchial spaces the liquid waste matter is likewise conveyed away in the outgoing respiratory current.

Excretory System. This consists of a pair of tubes, known as the organs of Bojanus, each communicating between the pericardium and the inner epibranchial chamber of its own side. Each opens into the anterior end of the pericardium by the **reno-pericardial aperture,** and runs posteriorly in the form of a tube with spongy walls. This turns dorsally, and the excretory organ then continues forwards in the form of an upper, thin-walled tube running parallel to the lower one. It opens into the inner epibranchial chamber by a **renal pore** a short distance in front of the point where the inner lamella of the inner gill becomes freed from the body-wall, the upper tube having first passed in an antero-ventral direction to cross the lower tube near its origin. The lower tube is definitely excretory in nature, the upper one functioning as a ureter for the removal of liquid waste products. Thus the excretory organs of the mussel closely resemble those of the crayfish, being in the form of tubes opening at one end into the cœlom and discharging their contents through the other end to the exterior. It should be noted also that in the anterior end of the pericardium there is a pair of bodies known as **Keber's organs.** These are of cœlomic origin and are excretory, casting their waste products into the pericardium, from which they are eliminated by the kidneys. Being of cœlomic origin they may be comparable to the chlora-

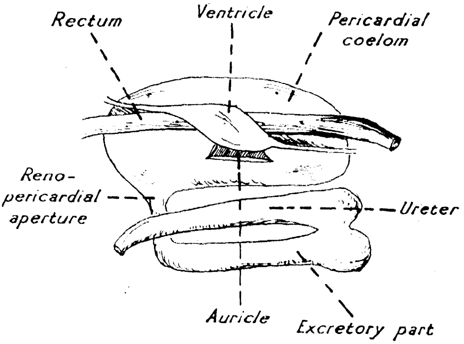


FIG. 61.—*Anodonta.* Cœlomic system.

gogenous cells of the earthworm, but the excretory function of the latter is not established. They may, in fact, be hepatic.

Nervous System. This is simply organised in *Anodonta.* It consists of a pair of **cerebral ganglia,** often known as the **cerebro-pleural ganglia,** since the pleural ganglia, usually found free in other bivalves, are believed to have become fused with the cerebral ganglia. They are strangely pigmented, being usually orange in colour, and are situated just behind the mouth. A pair of **pedal ganglia** in the foot is connected with the cerebro-pleurals by a pair of **cerebro-pedal commissures.** These two pairs of ganglia may be compared for positional relationship with the supra-pharyngeal and subpharyngeal ganglia of the earthworm. The nervous supply to the gut emanates from a pair of fused **visceral ganglia,** lying at the posterior end of the body and connected with the cerebro-pleural ganglia by a pair of **visceral commissures.** The sense organs of the mussel are poorly developed. No eyes are present. This is in marked contrast to other Mollusca—e.g. *Sepia*—where the eyes superficially resemble those of vertebrates. From each pedal ganglion in *Anodonta* a nerve passes a short distance posteriorly to supply a statocyst, resembling in structure that of the crayfish (page 80). The fused visceral ganglia are enclosed in sensitive epithelium, the organ so formed being termed an **osphradium.** The inhalant siphon is fringed with sensory tentacles, which are believed to test the purity of the water entering the respiratory chamber through that aperture. Should it be impure the siphon is closed and water already in the body is forced out.

Reproductive System. The sexes are separate, and the organs are similar in both male and female. The ovaries and testes are branching organs penetrating into the foot and opening on to each side by a duct whose aperture lies just below the renal pore, so that the genital products are shed first into the cavity of the inner gill, and so to the exterior. Spermatozoa, expelled through the exhalant siphon, enter the body of a female in the respiratory current through the inhalant siphon. Eggs are fertilised in the cloacal chamber, from whence they are passed to the space between the lamellæ of the inner gill, where early development takes place. A larva, known as a **glochidium,** is formed from each fertilised egg and set free in the following spring. It is enclosed in a bivalve shell, but the soft parts of the body include a foot in the form of a glandular mass of cells, from the middle of which passes a long, adhesive thread, known as the **byssus.** The mantle of the glochidium bears tufts of sensory hairs. The glochidium leads a free-swimming existence for only a short time, and eventually the byssus comes into contact with a small fish. The larva then embeds the teeth, found on the ventral edge of each valve of the shell, into the flesh of the fish, and settles down to live on it as a parasite, becoming at least partially enclosed as a result of inflammation of the tissues of the host. In this condition metamorphosis occurs, and the original larva now becomes converted into a miniature adult, which is then liberated from the host. Thus distribution is effected in a species which, in the adult stage, is of sluggish habits.

HELIX ASPERSA

Unlike *Anodonta* the snail is terrestrial and lives on vegetable food. It belongs to the phylum Mollusca and on the dorsal surface occurs a single, spirally-coiled shell, containing most of the viscera and into which most of the animal can be withdrawn. In winter the mouth of the shell is closed by a mucous secretion, which becomes hardened to form a plate known as an **epiphragm.**

External Features. The shell is in the form of a dextral (right-handed) spiral, new material being added during growth around the margin of the mouth of the shell until, in the adult, there are some four and a half turns. Projecting from the shell when the animal is in motion may be made out a head and a foot. The former is a rounded structure bearing two pairs of tentacles and situated at the anterior end of the body. The posterior or dorsal tentacles are the larger of the two, and each bears an eye at its free extremity. The anterior or ventral tentacles are smaller and arise just in front of and ventral to the dorsal ones. All the tentacles can be withdrawn each into an invaginated pit in the head. The foot is a large, muscular extension of the ventral surface of the body and is considerably expanded. At the anterior end it is rounded and reaches a position just below and behind the head, whilst posteriorly it becomes pointed. Along its under surface runs a median groove. Immediately within the mouth of the shell is a muscular **collar,** separated by a deep groove from the remainder of the body-wall. The mouth occurs at the anterior end of the head and on its ventral surface. A lateral lip may be seen on either side of it. Immediately below and behind the dorsal tentacle of the right side may be discovered the genital pore. From this

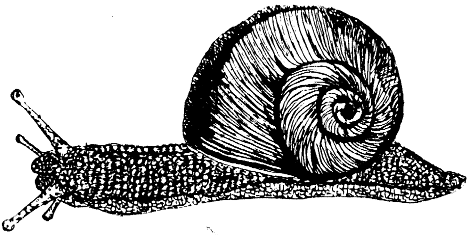


FIG. 62.—Garden snail.

there extends along the dorsal surface a groove, and the presence of a similar groove in an identical position on the left side suggests the descent of the snail from a symmetrical ancestor. Other apertures of importance are the pulmonary aperture, the anus and the opening of the pedal gland. The **pulmonary aperture** is situated dorsally in a groove lying in the right-hand side of the collar, whilst just to the right of and below this aperture lies the **anus.** Between the head and the foot in the middle line is the opening of the **pedal gland.** When the animal is removed from its shell a number of structures may be discerned from the outside. Thus the portion of the animal normally contained within the shell constitutes the **visceral hump.** One of the chief structures associated with this is the mantle. This is a fold in the body-wall, extending forwards along the dorsal surface to end anteriorly as the thickened **collar.** The space thus enclosed between the mantle and the body-wall forms the mantle cavity, communicating with the exterior by the pulmonary aperture, the mantle having become cemented down to the body-surface anteriorly but for this aperture. Lying opposite the collar may be made out beneath the skin a large, yellow, triangular structure. This is the **kidney,** whilst from this organ to the top of the spiral extends the **liver.** To the left of the anterior portion of the kidney occurs the pericardium in the form of an oval sac, whilst the **hermaphrodite gland** is situated as a small, yellow organ in the upper half of the second turn of the spiral (regarding the lowest one as the first).

Alimentary System. The mouth leads into a muscular pharynx, containing a toothed **radula** or **odontophore.** It is connected with the crop by a narrow, thin-walled œsophagus, whilst the crop itself is considerably expanded. Lying along the crop is a pair of salivary glands, whose ducts open into the pharynx. Immediately behind the crop lies a short stomach, which receives ducts from the right and left lobes of the liver. The latter is much the larger of the two and is subdivided into three, the three ducts uniting before entering the stomach. The intestine leads by a coiled course from the stomach to the rectum, which opens on to the surface on the right side near the pulmonary aperture.

Vascular System. The heart is situated in the pericardium, itself lying in the upper part of the mantle cavity. The heart is divisible into a thin-walled auricle, communicating with a thick-walled ventricle. From the ventricle there arises anteriorly an aorta to supply oxygenated blood to all parts of the body. From it a median visceral artery supplies the organs of the visceral hump, whilst a pedal artery is given off to the foot. The de-oxygenated blood is collected up into a number of sinuses. Thus there are two pedal sinuses in the foot and a visceral sinus in the visceral hump. Blood from these is conveyed to a pulmonary sinus in the region of the mantle cavity. From here it passes by a series of parallel, afferent pulmonary vessels to the roof of the mantle cavity, where oxygenation takes place. A number of efferent vessels unite to form a pulmonary vein along which blood is carried to the auricle, receiving on its course a renal vein from the kidney.

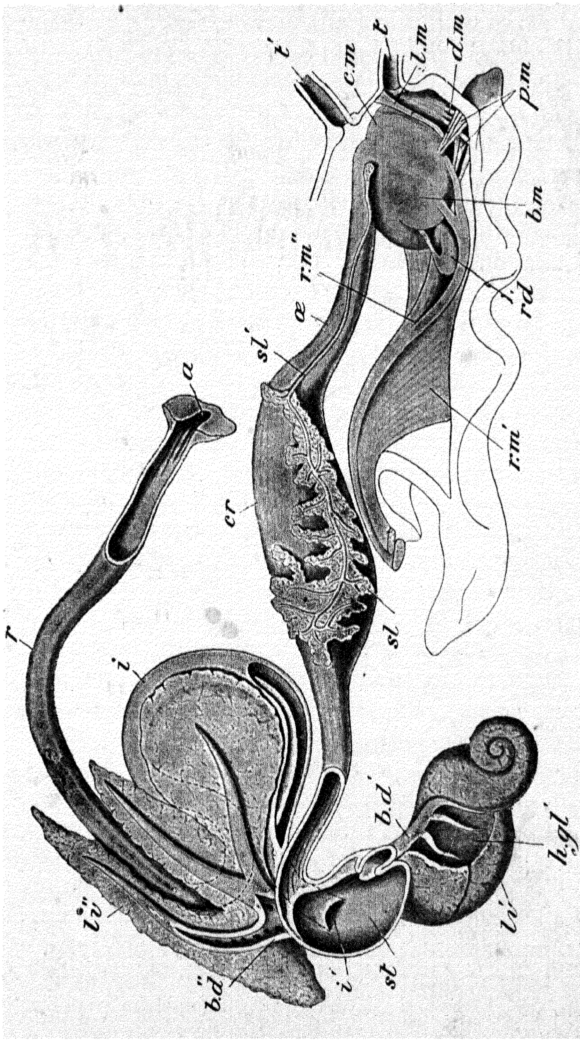


Fig. 63.—*Helix*. Alimentary system. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

a, anus; *b.d'*, right digestive duct; *b.d''*, left digestive duct; *b.m*, buccal mass; *c.m*, constrictor muscle; *cr*, crop; *d.m*, depressor muscles; *h.gl'*, depression for hermaphrodite gland; *i*, intestine; *i'*, intestinal orifice; *l.m*, levator muscle; *lv'*, digestive gland (right lobe); *lv''*, the same (left lobe); *œ*, œsophagus; *p.m*, protractor muscle; *r*, rectum; *rd*, radula sac; *r.m'*, retractor pedis muscle; *r.m''*, retractor buccalis muscle; *sl*, salivary gland; *sl'*, salivary duct; *st*, stomach; *t*, olfactory tentacle; *t'*, occular tentacle.

Nervous System. The ganglia of the nervous system are collected together to form a **nerve-collar** surrounding the pharynx, and are enclosed in a thick layer of connective tissue. When the head is protruded the pharynx is pushed forwards through the nerve-collar. Dorsal to the gut is a pair of **cerebral ganglia,** lying close together and supplying nerves to the tentacles and lips. Each is connected by a short buccal nerve with a **buccal ganglion** lying near to the opening of the salivary gland. The buccal ganglia are connected by a commissure. The subœsophageal ganglionic mass is connected by a pair of short commissures with the cerebral ganglia. The ganglionic mass consists of more or less fused pairs of pedal, visceral and pleural ganglia and is pierced by the anterior aorta. The sense organs of the snail are the eyes and auditory organs. Each eye is a hollow vesicle situated at the tip of a dorsal tentacle, and lined with retinal and pigmented cells. Within the cavity is found a large, refractive lens. The auditory organs occur actually embedded in the pedal ganglia in the form of small sacs, functioning similarly to the statocysts of *Astacus.*

Excretory System. This is built on the same plan as in *Anodonta,* except that there is only one kidney and ureter in *Helix.* The kidney opens into the pericardium by a reno-pericardial aperture and is itself a large, triangular organ situated in the posterior part of the roof of the mantle cavity. It is a glandular organ considerably subdivided by folds. At its end away from the pericardium a ureter occurs, whereby waste products are conveyed to the mantle cavity, into which they are discharged by a slit-like orifice near the pulmonary aperture.

Reproductive System. *Helix* is an hermaphrodite, but cross-fertilisation occurs. Both ova and spermatozoa are produced in a small hermaphrodite gland. The products are discharged along a convoluted duct, which opens into the base of an **albumen gland.** From this latter organ passes a single duct, though this becomes divided by a constriction into separate male and female channels. At the anterior end the two channels become completely separated to form **a vas deferens** and an **oviduct.** From the vas deferens arises a long, hollow diverticulum, known as a **flagellum,** within which spermatozoa are cemented together to form spermatophores. The vas deferens terminates in a muscular penis, from which sperms are discharged to the genital pore. The oviduct soon widens to form a **vagina,** into which open two mucous glands, each very much subdivided. Nearer the genital pore there arises from the vagina a **dart sac,** containing a calcareous **style,** believed to be used for stimulation to coition. From the base of the vagina arises a blind diverticulum, which becomes considerably swollen at its free end. This is the **spermatheca,** and from it there projects a further blind,

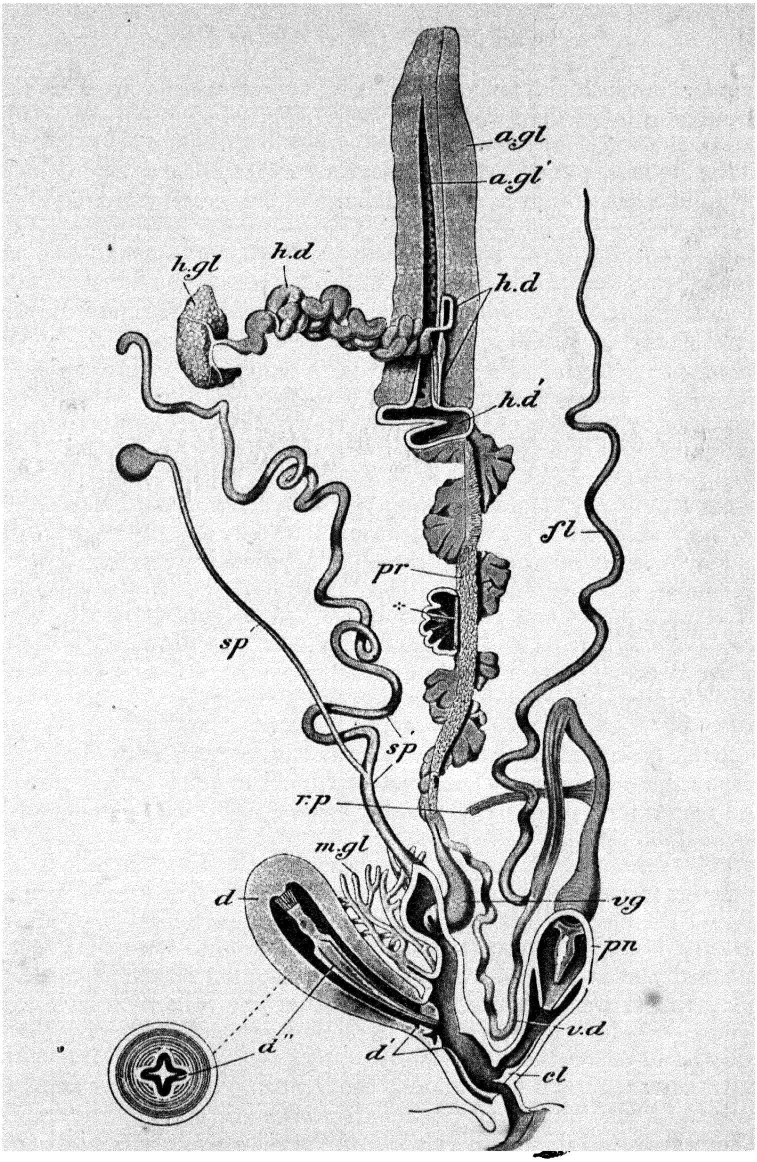


Fig. 64.—*Helix.* Reproductive organs. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

a.gl, albumen gland; ***a.gl'***, duct of same, laid open; ***cl***, genital cloaca; ***d***, dart sac; ***d'***, valvular lip of same; ***d''***, the dart; ***fl***, flagellum; ***h.d***, hermaphrodite duct, first segment; ***h.d'***, the same, sacculated segment; ***h.gl***, hermaphrodite gland; ***m.gl***, mucous gland; ***pn***, penis; ***pr***, accessory gland; ***r.p***, retractor penis muscle; ***sp***, spermotheca; ***sp'***, diverticulum of same; ***v.d***, male duct ("vas deferens"); ***vg***, female duct (vagina); ✛, fold exposed in hermaphrodite duct.

tubular outpushing, longer than the actual spermatheca itself. Copulation takes the form of an interchange of spermatozoa as in the earthworm, and the sperms are stored in the spermatheca.

The Molluscan Shell. The Molluscan shell is formed of an organic, chitin-like basis, known as **conchiolin.** This becomes hardened by the deposition of salts of lime. It is composed of three layers. On the outside is the **periostracum,** consisting of conchiolin only and wearing away with age. Within this is a calcified layer. This is usually thick and laminated, and is called the **prismatic layer.** Finally, on the inside, is the **nacreous layer,** forming the so-called "mother of pearl." Its iridescent colours are due to interference caused by fine striations on the surface. All three layers are produced by the edge of the mantle, though the innermost is formed by the general dorsal surface of the body. It is the only layer of shell present in the larva.

The Mollusca. Members of the phylum Mollusca are characterised by the possession of an unsegmented, bilaterally symmetrical body, and by the presence of a calcareous dorsal shell overlying a soft epidermis, not covered by a cuticle. The hæmocœl is large in the adult and the cœlom relatively restricted, being confined to the pericardium, gonads and excretory organs. The principal ganglia of the nervous system lie close together at the anterior end, and the commissures joining them surround the gut. The body is normally extended ventrally in the form of a foot, whilst down-growths from the dorsal surface form the mantle, bordering the respiratory chamber. The blood-vascular system is open, whilst the respiratory pigment is usually hæmocyanin but occasionally hæmoglobin.

This primitive structure has become variously modified in different forms. Thus in the class Lamellibranchiata, to which the mussel belongs, the mantle cavity contains highly-specialised gills, already described, whilst the shell has come to consist of two lateral, calcified plates. In the Gastropoda, represented by the snail, the body has become spirally twisted, so that the primitive, bilateral symmetry is obscured. In the Cephalopoda part of the foot has become incorporated with the "head," this region of the foot bearing suckers and surrounding the mouth. The shell is at first external, but later undergoes reduction and becomes internal. They are the dominant marine invertebrate group, and are exemplified by the octopus.

becomes enlarged to form the axial organ. At its aboral end this is in connexion with an aboral hæmal ring, from which a branch passes to each pair of gonads.

The systems above described are all concerned with respiration, distribution and excretion. They may be classed together as the conducting systems.

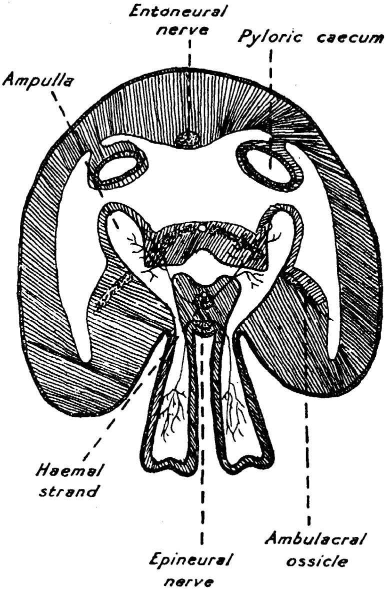


FIG. 66.—*Asterias.* Section of arm.

Nervous System. This is essentially divisible into three components.

(*a*) *The Ectoneural.* This takes the form of a ring surrounding the mouth, and from it radial nerves are given off to the eyes, tube-feet and skin generally. There is an eye situated at the end of each radial, water-vascular canal, and each consists of seven facets, each covering a pigmented cup with a layer of retinal cells below.

(*b*) *The Hyponeural.* This also consists of a ring around the mouth, giving off a pair of nerves along each radius to supply the deeper layers of the body-wall.

(*c*) *The Entoneural.* This is made up of a number of radial nerves meeting at the centre, and is aboral in position.

Reproductive System. The sexes are separate and similar in appearance. There are five pairs of gonads, situated one in each arm, and connected by ducts with five pairs of inter-radial genital pores.

The Echinoderma. Members of this phylum are exclusively marine. Their development shows that a form of radial symmetry has been superimposed on a bilateral symmetry. In some forms a bilateral symmetry is again superimposed on this. They have a mesodermal skeleton composed largely of calcite. It is of interest to note that the individual spicules polarise light, this frequently enabling a fossil to be identified as an Echinoderm, though sponge spicules also have this property. The cœlom is well represented, and development of the organisms in this phylum is accompanied by considerable metamorphosis.

CHAPTER XII

AMPHIOXUS AS A PRIMITIVE CHORDATE

Amphioxus lanceolatus is an animal of great significance, since it exhibits many chordate features at a primitive stage of development. It will be as well at the outset, therefore, to investigate in what respects the vertebrates resemble and differ from the higher invertebrates, so that these characters can be borne in mind when studying the following vertebrate types. Thus both vertebrates and the higher invertebrates are cœlomate, bilaterally symmetrical Triploblastica and are metamerically segmented. But a vertebrate is distinguishable from a higher invertebrate by several diagnostic features. Thus, a vertebrate possesses a **notochord.** This is an elastic rod functioning as a skeletal support and primitively extending throughout the entire length of the animal. In almost all forms it becomes more or less completely invaded and replaced in later life by cartilage or bone. Respiration is primitively effected by gill-slits. In higher vertebrates these structures become very largely suppressed, but rudiments still persist in the form, for example, of the Eustachian tube of Tetrapoda. Blood is maintained in motion in vertebrates by a ventral heart through which blood flows forwards. It will be remembered that blood flows forwards in the dorsal vessel of the earthworm, for instance. The main skeleton of a vertebrate is internal, whereas an exo-skeleton is common in invertebrates, especially in the Arthropoda. By a series of ingrowths from this structure a type of internal skeleton may be formed, as exemplified in the endophragmal skeleton of *Astacus*, though this is in no way homologous with the endoskeleton of vertebrates. Appendages in the invertebrates are typically arranged one pair per segment, though limbless segments occur. Vertebrates bear appendages, each of which arises from a number of segments. The nerve-cord of a vertebrate is typically hollow and is dorsal in position. It will be remembered that in the earthworm reference was made to the beginnings of differentiation of nerve fibres into sensory (afferent) and motor (efferent). In vertebrates this differentiation has been carried to such an extent that a nerve at its entry into the spinal cord becomes divided into two roots, described as dorsal and ventral, and composed of afferent and efferent fibres respectively. In the head region these roots have become separated, as will be seen in Chapter XXIII. With the progress in development of the blood-vascular system in vertebrates, portal systems are observed. A portal system is a composite blood-vessel commencing and terminating in the form of capillaries. Thus, in vertebrates there occurs consistently an hepatic portal system composed of vessels with their origin in the intestine, from which they pass as a single vessel, breaking up again in the liver. Finally, it may be mentioned that the skeletal rod, giving place later to the vertebral column, is normally extended beyond the anus to form a true tail. These characteristics are amply illustrated in *Amphioxus*.

External Features and Body-wall. *Amphioxus lanceolatus* is a small, fish-like organism found burrowing in the sand forming the bottom of shallow seas, only the mouth being normally visible.

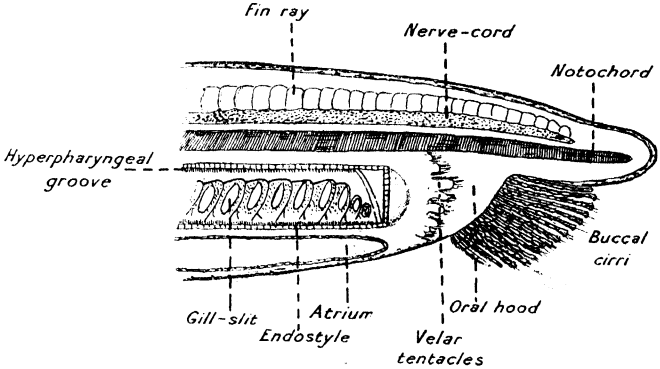


FIG. 67.—*Amphioxus*. Anterior end.

The animal is laterally compressed, and pointed at either end. Along the entire dorsal surface is a shallow fin connecting small fins at the two ends. A fin extends for a short distance from the tail along the ventral surface. All these fins are supported by stiffening rods, known as fin-ray boxes. These are, however, not segmental in origin, being more numerous than the segments. They are composed of connective tissue. At the anterior end the ventral surface is compressed into the dorsal and expanded to form the **oral hood.** At the sides of this structure there is a number of **buccal cirrhi,** each supported by a small, jointed, skeletal rod. The epidermis of the under surface of the oral hood has become ciliated to form a structure known as the **wheel organ.** By the beating of its cilia a current of water is driven towards the mouth. To the right of the middle line of the oral hood opens a small depression, known as **Hatschek's pit,** the significance of which is discussed in Chapter XVII. Near the front end of the body on the left-hand side opens the **olfactory pit.** Lying at the hind end of the oral hood is a flap of skin, known as the **velum** and bearing twelve sensory velar tentacles. These act as a strainer across the mouth, which is itself a circular orifice in the velum and closeable by a sphincter muscle. *Amphioxus* possesses a short tail, so that the anus lies some little distance from the posterior end and on the ventral surface. Owing to the position of the ventral fin in that region the anus opens to the left of the middle line. Lying just in front of the anus is a median **atriopore,** the significance of which will be considered later. The skin of *Amphioxus,* as in all vertebrates, is divisible into a superficial epidermis of ectodermal origin, whilst beneath it occurs a mesodermal dermis, usually containing blood-vessels. The epidermis of *Amphioxus* is but a single cell thick, in which respect it resembles that of many invertebrates. The dermis of *Amphioxus* is nothing more than a gelatinous mass of connective tissue. The majority of the mesoderm is in the form of segmental muscle-blocks or **myomeres** which are visible through the skin as V-shaped structures directed forwards. These are covered with cœlomic epithelium and are separated from the endodermal gut by a spacious cœlom.

The Atrium. From a region just behind the oral hood and for just over half the length of the animal the body-wall has become curiously folded to form a chamber, known as the **atrium,** enclosing the gill-slits and opening to the exterior by a median atriopore just in front of the anus. The atrium is formed from a pair of longitudinal folds (metapleural folds), which arise one just above the gill-slits on either side of the body. They proceed to grow ventrally, and, when they have grown to a level just below the ventral surface, shelves (epipleural folds) extend inwards from their inner walls towards the middle line, and these shelves eventually fuse. Thus the atrium is a cavity lined entirely by ectoderm and enclosing a portion of the outside world around the animal in the region of the gill-slits. At the front end the metapleural folds become cemented down to the true surface of the animal so that anteriorly the atrium is completely closed, whilst posteriorly on the right-hand side it is extended backwards in the form of a blind diverticulum reaching almost to the anus. Connecting the cœlom of the posterior pharyngeal region with the atrium is a pair of " brown " funnels.

Alimentary System. The alimentary canal of *Amphioxus* is a straight tube leading from mouth to anus. It is regionally differentiated into two portions only, namely, an anterior **pharynx**

and a posterior intestine. The majority of the gut is ciliated and a muscular coat assists in forcing the food along. The pharynx is perforated by about one hundred and eighty gill-slits which slope forwards from their ventral to their dorsal margins. It must be clearly understood that a gill-slit is a cavity communicating between the pharynx and the exterior, whereas a gill is the name applied to the richly-vascularised folds of the walls of the gill-slits. In the case of *Amphioxus* the gill-slits communicate not with the exterior in the true sense but with the atrium. *Amphioxus* is primitive in that it portrays a ciliary mode of feeding. The cilia on the oral hood have already been referred to, and, once inside the pharynx, the food is still very largely controlled by ciliary action. Running along the ventral surface of the pharynx is an highly-specialised, ciliated apparatus known as the **endostyle.** This consists of four tracts of ciliated cells arranged in a half-hoop and separated from each other by a similar number of tracts of gland cells. These produce a mucous secretion to which particles of food become attached. In this condition they are carried forwards, perhaps to the extreme anterior end of the endostyle. Here this ciliated band forks and the two branches (**peripharyngeal bands**) pass one up either side of the pharynx to become united again dorsally. In this way they give rise to the **hyperpharyngeal groove** running along the dorsal side of the pharynx. The food is carried in a stream of mucus up the peripharyngeal bands to the hyperpharyngeal groove, along which it is conveyed backwards to the intestine. Not all the food passes up these peripharyngeal bands, however, for the gill-bars (the rods of tissue separating the gill-slits) are ciliated and may be made use of to convey the food from the endostyle to the hyperpharyngeal groove. It will be observed that in this way particles of food are prevented from passing out in currents of water through the gill-slits, but at the same time such a mechanism is obviously of use only in small animals where the food particles are of such a size as to facilitate their being carried in a stream of mucus. Thus in higher forms this ciliary apparatus has become superfluous, and mention will be made in Chapter XXIX of its evolutionary fate,

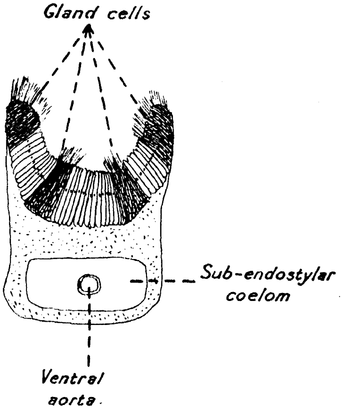


FIG. 68.—*Amphioxus.* Section of endostyle.

as well as that of the wheel organ in the oral hood. The intestine bears at its anterior end a blind diverticulum known as the "liver," and the whole gut is suspended by a dorsal mesentery, the significance of which will be made clear when the development of *Amphioxus* is studied (Chapter XVII).

Respiratory System. Early in life the gill-slits are segmental in arrangement, but later they become very much subdivided. The gill-slits are separated from each other by gill-bars, each strengthened by a skeletal rod. The gill-bars separating the original segmental gill-slits are described as primary, whilst those arising later in life are called secondary gill-bars or **tongue-bars.** The primary gill-bars may be distinguished from the secondary in that the rods of the latter end simply at their ventral extremities, whereas those of the primary ones are bifurcated. Furthermore, the primary bars contain an extension of the cœlom, which is absent from the tongue-bars. All the bars are thickly ciliated, and by this means a stream of water which enters by the mouth is forced through the gill-slits into the atrium. As this is taking place the dissolved oxygen is absorbed into the blood in the vascularised diverticula of the walls of the gill-slits and waste carbon dioxide is eliminated from the blood. The residual water passes to the exterior through the atriopore. Each primary gill-bar contains three blood-vessels and each tongue-bar two. The primary and secondary gill-bars are connected by synapticula in which run communicating blood-vessels.

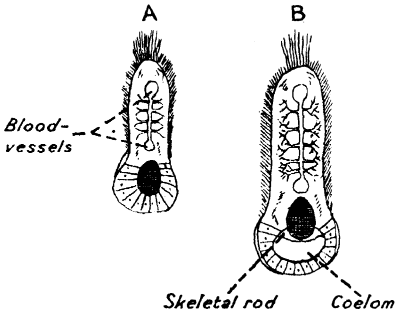


FIG. 69.—*Amphioxus.* Gill-bars. A. Secondary. B. Primary.

Vascular System. *Amphioxus* has no clearly-differentiated heart, but the plan of its blood-vascular system is typically piscine. Ventral to the pharynx in the endostylar region is a **ventral aorta.** This is contractile in nature and forces blood forwards through the **afferent branchial arteries** into the primary gill-bars. The secondary gill-bars have no direct blood supply of their own, deriving it from the vessels of the primary bars through the **synapticula.** Just previous to entering a primary gill-bar each afferent branchial artery becomes enlarged to form a small bulbil, from which three vessels emerge to supply the bar. The oxygenated blood is then collected up into a number of **efferent branchial arteries.** These unite on each side to form a **lateral dorsal aorta** in the region of the hyperpharyngeal groove. These pass backwards and unite just behind the pharynx to form a **median dorsal aorta,** from which blood is supplied to the posterior region of the body by means of inter-segmental vessels. Running forwards beneath the ventral surface of the intestine is a **sub-intestinal vessel,** into which all the blood of that region is collected up. This vessel breaks up again into capillaries in the liver diverticulum, and thus there is formed an hepatic portal system. From the liver capillaries become

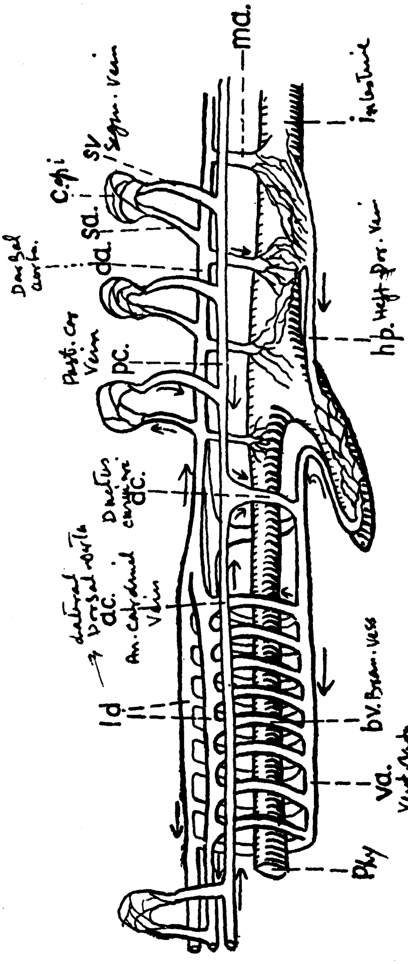


FIG. 70.—*Amphioxus.* Diagram of vascular system. (From "Vertebrate Zoology," by G. R. de Beer.)

ac., anterior cardinal vein; *bv.*, branchial vessel in gill-bar; *c.*, capillaries; *da.*, dorsal aorta; *dc.*, ductus Cuvieri; *hp.*, hepatic portal vein; *i.*, intestine; *ld*, lateral dorsal aorta; *ma.*, artery running in mesentery and supplying the gut; *p.*, pharynx; *pc.*, posterior cardinal vein; *sa.*, segmental artery; *sv*, segmental vein; *va.*, ventral aorta.

reunited to form a vessel which runs forwards again, merging into the ventral aorta. Besides the sub-intestinal vein, there is also a pair of **lateral veins** running in the body-wall and extending from the region of the pharynx to the tail. They are connected with the sub-intestinal vein just before this becomes the ventral aorta (i.e. after it has left the liver diverticulum) by a pair of **ductus Cuvieri** running across the cœlom.

The Skeleton. *Amphioxus* is supported by an elastic notochord extending from the extreme anterior to the extreme posterior end. It is situated dorsal to the gut and ventral to the nerve-cord. The buccal cirrhi and the gill-bars are each supported individually by skeletal rods, as already mentioned.

Nervous System. In *Amphioxus* there is a well-developed central nervous system consisting of a dorsal, tubular nerve-cord extending throughout the length of the animal. At its anterior end the lumen becomes enlarged to form the cerebral vesicle, but as there is no change in the external diameter of the tube it follows that the wall in this region must have become thinner. Pairs of dorsal and ventral nerve-roots emerge from this dorsal nerve-cord during its passage along the animal. These nerve-roots are arranged segmentally, each segment containing a pair of dorsal roots and a pair of bunches of ventral roots. As in higher vertebrates, each ventral root innervates the musculature of its particular segment, whilst the dorsal root receives sensory impulses from the skin, as well as supplying the muscle of the gut and atrium. The axons comprising the fibres of the dorsal root are derived from sensory cells of the skin by extension inwards to penetrate the nerve-cord. This is strictly comparable to the origin of sensory nerve-fibres in many Invertebrata—e.g. the earthworm. It will be found in higher vertebrates that the axons comprising dorsal roots are derived from true nerve cells, the cell-bodies of which lie just outside the nerve-cord. The collection of cell-bodies associated with any one dorsal root is known as a dorsal-root ganglion. The skin is then supplied by extensions from each cell-body, so that the cell-bodies lie at the opposite end of the axon in higher forms to that in *Amphioxus*. The anterior end of *Amphioxus*, owing to the presence of buccal cirrhi and oral hood, is particularly sensitive, and thus the first two pairs of nerves consist of dorsal roots only with no corresponding ventral roots.

The Cœlom. The structure of the cœlom may best be understood by tracing its development in *Amphioxus*. This is done in Chapter XVII. For the present it is sufficient to say that in the intestinal region the gut is supported in a spacious cœlom by a dorsal mesentery. But in the pharyngeal region the position is complicated by the

CHAPTER XIII

SCYLLIUM

THE characteristic features of the Chordata have already been pointed out in Chapter XII, and the following types will serve to illustrate them. There are a few classes at the base of the Chordate stock, containing such forms as *Amphioxus* and the Cyclostomes. The five classes of the Chordata with which we shall now be concerned are grouped together in the branch Gnathostomata, characterised, as this term suggests, by the presence of jaws. The classes in question are the Pisces, Amphibia, Reptilia, Aves and Mammalia. The chief characteristics of three of these will be illustrated by the detailed description of a type, namely, *Scyllium*, *Rana* and *Lepus*, whilst the external features and skeleton of *Columba* (the pigeon) will be dealt with. Occasional reference to structural features in the Reptilia will be made in subsequent chapters. It is assumed that before reading this chapter the student will already have studied the frog.

External Features. The dogfish, in reality a small shark, occurs round the British coast, where the commonest species, *Scyllium* *canicula* (the Lesser Spotted dogfish), preys on almost any form of animal food, though living principally on Crustacea. It derives its name from the fact that hunting is done in packs and is largely facilitated by its keen sense of smell. The body is some two feet in length, and a distinct head and tail may be discerned. The head is compressed dorso-ventrally, and on the ventral surface near the front end is a crescentic mouth. Just in front of the mouth is a pair of nostrils, whilst situated laterally on the head is a

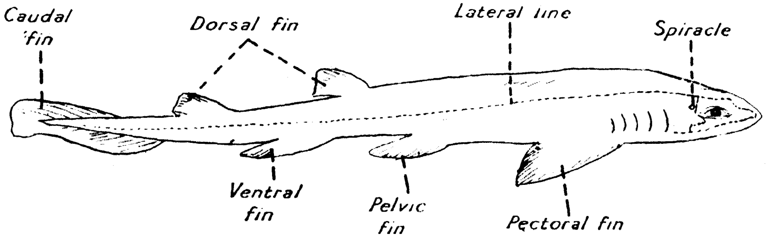


FIG. 74.—*Scyllium*. Externals.

pair of slit-like eyes. On each side of the body just behind the head are six small openings, leading into tubes communicating with the pharynx. These are the gill-slits. The first one is much smaller than the rest and is situated more dorsally, lying immediately behind the eye ; it is known as the **spiracle.** The trunk, especially posteriorly, is laterally compressed, and bears a number of fins. There is a pair of pectoral fins arising just behind the head. They are ventro-lateral in position and correspond to the fore-limbs of Tetrapoda. The pair of pelvic fins lies behind the pectorals and they arise close to the mid-ventral line. They are smaller than the pectoral fins, and in the male their inner edges are fused, whilst there projects backwards from the under surface of each a grooved rod, known as a clasper. This is the only means of external distinction between male and female. As well as the paired fins already described, there is a number of median fins. Arising about one-third of the length of the animal from the hind end is a small, anterior, dorsal fin, whilst a short distance behind this is the posterior, dorsal fin. Between the positions occupied by these two fins, but on the ventral surface, is a small, ventral fin. The tail is enveloped by a vertical caudal fin, of which the ventral lobe is slightly larger than the dorsal. The cloaca is situated in the mid-ventral line between the pelvic fins, and on either side of it is a minute abdominal pore, communicating with the cœlom. The whole surface is covered with sharp spines, directed backwards and known as denticles or placoid scales. Each of these consists of a mass of dentine, produced by the dermis, and covered with a cap of enamel secreted by the ectoderm. As will be seen later, this is very like the structure of a tooth of higher forms. In fact, in the dogfish similar but slightly enlarged scales around the margin of the jaws function as teeth. Running along on either side of the body may be distinguished faint lines. This is the lateral line, which will be dealt with in greater detail later (page 125).

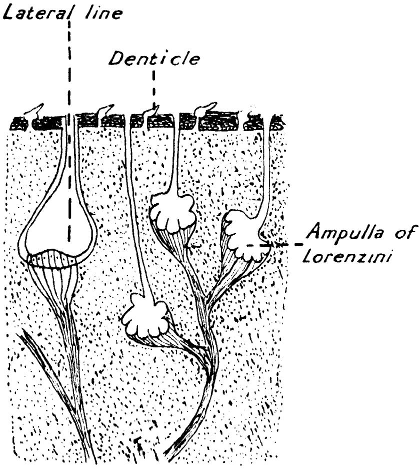


FIG. 75.—*Scyllium.* Vertical section of skin.

The Skeleton. The skeleton of the dogfish consists entirely of cartilage. It is typically divisible, as is that of other Gnathostomata, into an axial skeleton, consisting of skull and vertebral column, and an appendicular skeleton, made up of limb-girdles and limbs. It is essential to bear in mind throughout that the animal is segmented, and this is readily appreciated if the myomeres (muscle-blocks) are examined after the removal of the skin. They do not lie straight across the body, but are characteristically W-shaped. In the head the segmental arrangement of the muscles is obscured.

(A) Vertebral Column. The notochord, persistent throughout life in *Amphioxus*, has become very largely replaced by cartilage. Some 130 vertebræ are formed by invasion of this rod. Each consists of a **centrum,** formed from a pair of **basidorsal cartilages** (above) and a pair of **basiventral cartilages** (below), which become fused to give rise to a ring-like structure enclosing the notochord. The canal through the centrum is at its smallest in the centre and widens towards each end. The centra articulate with each other end to end, and from each centrum there arises on either side a neural arch. The pair of arches from each centrum fuse above in the mid-dorsal line to enclose a canal through which runs the nerve-cord. Between the neural arches of successive vertebræ are **interdorsal cartilages,** whilst in the tail region the basiventrals

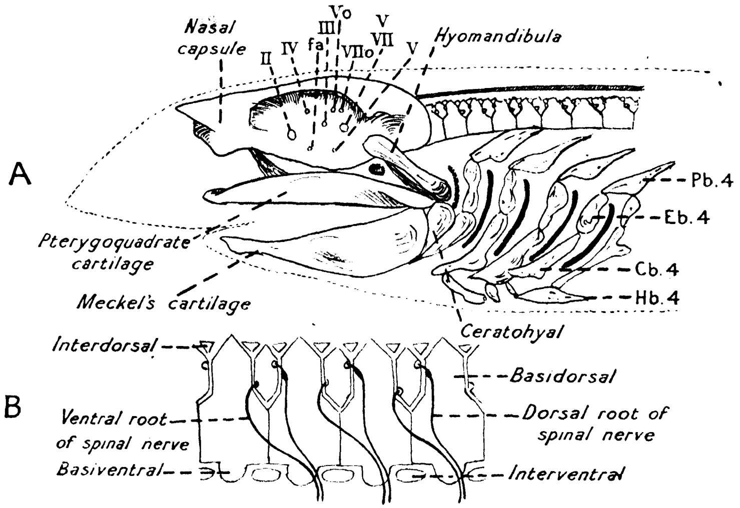


Fig. 76.—*Scyllium*. A. Skull. B. Vertebral column.
Pb.4 = pharyngobranchial; Eb.4 = Epibranchial; Cb.4 = ceratobranchial; Hb.4 = hypobranchial; II–VII = cranial nerves; fa = foramen for artery. 4 indicates fourth branchial arch.

become extended ventrally on either side to give rise to **hæmal arches.** In the trunk region short ribs are formed by lateral extensions of the basiventrals. Each centrum is actually inter-segmental in position.

(B) SKULL. This is essentially a cartilaginous case, known as the **cranium** and containing the brain. On to the front end is fused a pair of **nasal capsules,** whilst at the hind end occurs a pair of **auditory capsules.** The nasal capsules themselves are open below and their cavities are separated from each other by a **mesethmoid cartilage.** At the extreme anterior end is found a **rostrum,** formed by three processes projecting each from a nasal capsule and the mesethmoid cartilage. The cranium completely envelops the brain except for an aperture in the roof, known as the **anterior fontanelle** and situated at the line of fusion with the nasal capsules. Placed laterally in the cranium is a pair of orbits, each protected by a supra-orbital and sub-orbital ridge in the cartilage. Posteriorly the auditory capsules are continuous with the cranium, and on their surface is indicated the position of the semi-circular canals of the ear, later to be described, whilst just on either side of the mid-line and between the capsules lies a small pore communicating by a duct with the ear of its own side. The notochord has become completely replaced in the skull region, and an articulation is developed between the posterior region of the skull and the anterior end of the vertebral column. The brain being thus enclosed within the cranium special apertures, known as foramina, must be pierced in the cartilaginous case to allow of the passage of nerves to and from the brain, as well as for facilitating a supply of blood to this organ. The disposition of these foramina is indicated in Fig. 76. The structure so far described is known as the **neurocranium,** in contradistinction to the **splanchnocranium** or visceral skeleton, itself consisting of seven pairs of composite arches attached by ligaments to the neurocranium or vertebral column. The skeleton of the jaws is formed from the first or mandibular visceral arch. The upper jaw consists of two **pterygo-quadrate**

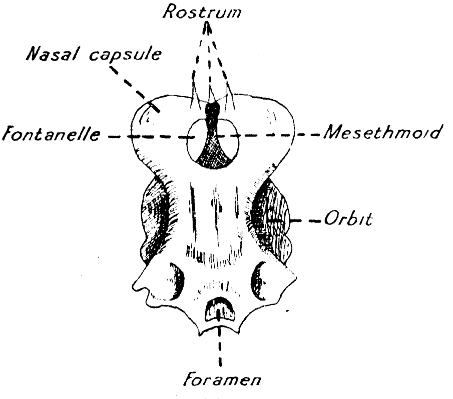


FIG. 77.—*Scyllium.* Dorsal view of skull.

cartilages, joined anteriorly in the middle line by ligaments. It is attached to the neurocranium by two pairs of ligaments. The lower jaw consists of a pair of **Meckel's cartilages,** also joined to each other anteriorly by a ligamentous connexion, and articulating posteriorly with the hind end of the pterygo-quadrate cartilages. The second arch is known as the **hyoid** and consists on each side of two pieces—the **hyomandibula** and the **ceratohyal.** The hyomandibula articulates at one end with the outer face of the auditory capsule, whilst to its other end is attached by a ligament the pterygo-quadrate cartilage of that side. The ceratohyal cartilage also articulates with the distal end of the hyomandibula, whilst the ceratohyal from each side passes forwards to join the basihyal, a medial cartilaginous plate in the floor of the mouth.

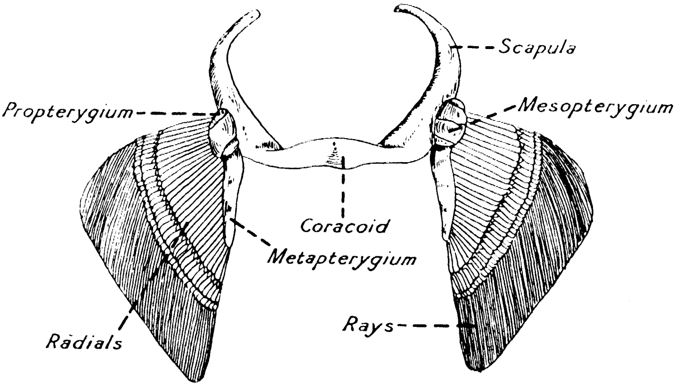


Fig. 78.—*Scyllium.* Pectoral girdle.

The remaining five arches are known as the branchial arches, an each consists of four parts, named (from the vertebral colum downwards) the **pharyngobranchial, epibranchial, ceratobranchia** and **hypobranchial,** disposed as shown in Fig. 76. The pterygo quadrate and the hyomandibula represent the epibranchials o their respective arches, whilst the Meckel's cartilage and th ceratohyal correspond to the ceratobranchials of subsequen segments. The partitions between the gill-slits are strengthene by **extrabranchials** and gill-rays emanating from the lower element of the branchial arches.

The mode of attachment of the pterygo-quadrate to the neuro cranium by means of ligaments and the hyomandibula is importan and is described as **hyostylic.**

(C) Fins. The paired fins are anchored to the body by a **pectora** and **pelvic** girdle and are supported by cartilaginous radials. Th pectoral girdle consists of a half-hoop of cartilage, divisible int a median **coracoid** and a pair of **scapular** regions at the free, upward-directed extremities. On each side is a facet, known as the **glenoid cavity,** separating the coracoid from the scapular region of each side, and into which the fins are articulated. Each fin consists of three proximal cartilages, known (passing inwards) as the **pro-, meso-** and **meta-pterygia.** Articulating with these is a large number of jointed radials.

The pelvic girdle is a cartilaginous rod lying transversely in the body-wall. At each end it articulates with a **basipterygium,** which itself bears a number of jointed radials along its anterior border.

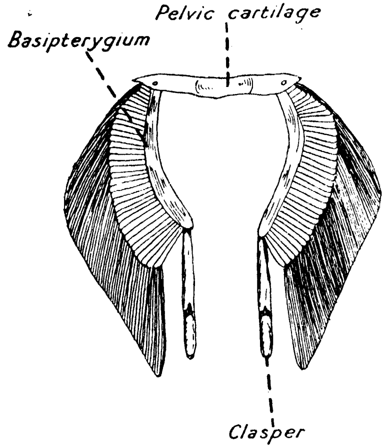


FIG. 79.—*Scyllium.* Pelvic girdle.

The median fins are also supported by jointed, cartilaginous radials, more numerous than the segments. The webs of all the fins are themselves supported by dermal fin-rays or ceratotrichia, very much more numerous than the radials which bear them.

Alimentary System. From the mouth the food passes into the **pharynx.** This organ is perforated by the five pairs of gill-slits and the spiracles. But the food is normally too large to be lost through them. The pharynx leads into a narrow **œsophagus,** communicating with a U-shaped **stomach.** The proximal (first) arm of this organ is known as the **cardiac** region, whilst the distal limb is the **pyloric** region and is narrower. This is separated from the cavity of the intestine which follows by a **pyloric sphincter** muscle. A sphincter muscle is one surrounding an orifice, and which, under normal conditions, is closed, only to be opened at intervals. Thus the muscle of the mammalian anus is a sphincter muscle. Immediately beyond the sphincter muscle is a very short, somewhat narrow region, known as the duodenum or **bursa entiana.** Following this is the intestine or **ileum,** a wide-tube leading straight but for one curve to the cloaca. The internal surface of the ileum is increased by a fold in the lining of the epithelium, known as the **spiral valve.** At its posterior end the ileum narrows and loses its spiral valve to form the **rectum.** The liver is a large, bi-lobed structure attached to the cœlomic wall by the **falciform ligament.** The gall-bladder is largely embedded in the under surface of the left lobe, and from it the bile-duct runs backwards to open into the bursa entiana. The **pancreas** lies in the bend between the stomach and the intestine. At its anterior end is a rounded lobe, from which a pancreatic duct enters the bursa entiana. The **spleen,** though not a digestive organ, is in close connexion with the stomach. It is a small, triangular structure, situated at the base of the U-shaped stomach and with one arm projecting along the right side of the pyloric limb. A small, dorsal diverticulum from the rectum constitutes the **rectal gland.** The process of digestion is described in detail in the chapter on the frog, and in principle it is the same in all Chordata. It should be noted that no saliva is present in the

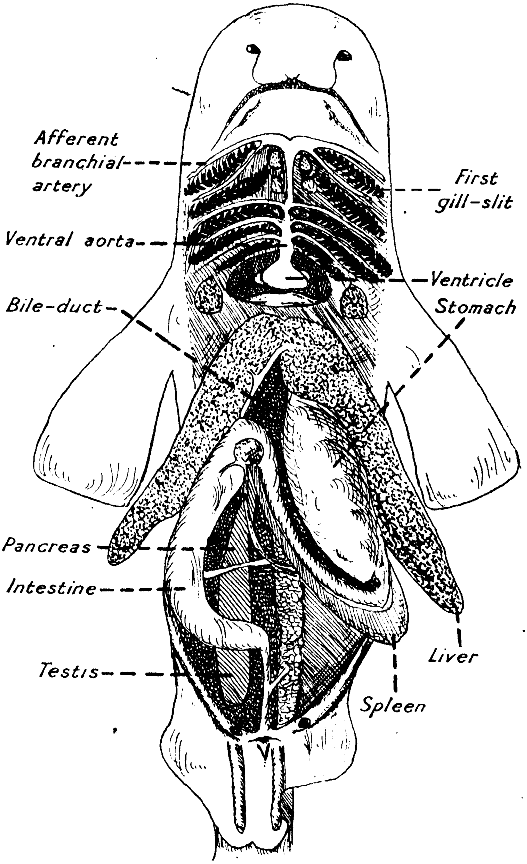


FIG. 80.—*Scyllium.* Afferent arterial system and alimentary system.

fish, since it would get washed out through the gill-slits in the respiratory current.

Respiratory System. As has already been mentioned, the pharynx is perforated by five pairs of gill-slits and a pair of spiracles, communicating between it and the exterior. These gill-slits slope backwards from their inner to their outer openings. The cavities of the gill-slits become enlarged within and each wall (anterior and posterior) bears a number of richly vascularised folds. These constitute the gills. The walls separating the gill-slits are supported by the skeleton of the visceral arches, the first true gill-slit (not the spiracle) lying between the hyoid and the first branchial arch, whilst the spiracle occurs between the mandibular and hyoid arches. The last gill-slit and the spiracle each has a gill on its anterior wall only, that of the spiracle being termed a **pseudobranch.** The arches lying immediately in front of each gill-slit (including the spiracle) and behind the last are known as the visceral arches, and are named the mandibular, hyoid and first to fifth branchial arches, as already indicated in the description of the visceral skeleton.

Respiration is effected by the taking in of water through the mouth and its being forced out through the gill-slits. During its passage over the gills the blood becomes oxygenated, whilst waste carbon dioxide is passed into the water and removed. The respiratory pigment of the blood of the dogfish is hæmoglobin.

Vascular System. The vascular system is built on the same plan as in *Amphioxus*. The heart lies in the **pericardium,** situated in the middle line between the posterior gill-slits. It is essentially an S-shaped structure. Posteriorly there is a thin-walled **sinus venosus** into which is drained all the deoxygenated blood from the whole body. This chamber communicates anteriorly with a somewhat thicker-walled **auricle,** itself opening into a very thick-walled **ventricle.** From this passes forwards a narrow **conus arteriosus,** which penetrates the front wall of the pericardium to become the **ventral aorta.** Valves are situated at intervals in the heart to prevent the blood from "sucking back." The openings between the sinus venosus and the auricle, and auricle and ventricle, are thus guarded, whilst a double row of semi-lunar valves occurs in the conus.

(A) Arterial System. Five pairs of **afferent branchial** arteries arise from the ventral aorta to supply blood to the gills. They run in the fourth, third, second and first branchial arches, whilst the most anterior one supplies the hyoid arch (behind the spiracle). After oxygenation at the gills the blood is collected up into four pairs of **efferent branchial** arteries. These form loops enclosing each of the first four pairs of gill-slits (not including the spiracle). Since the last gill-slit has no gill on its posterior wall it has an efferent vessel along its anterior margin only, and from this blood is conveyed to the loop round the gill-slit next in front. From the dorsal end of each loop blood is conveyed away by an **epibranchial** artery to

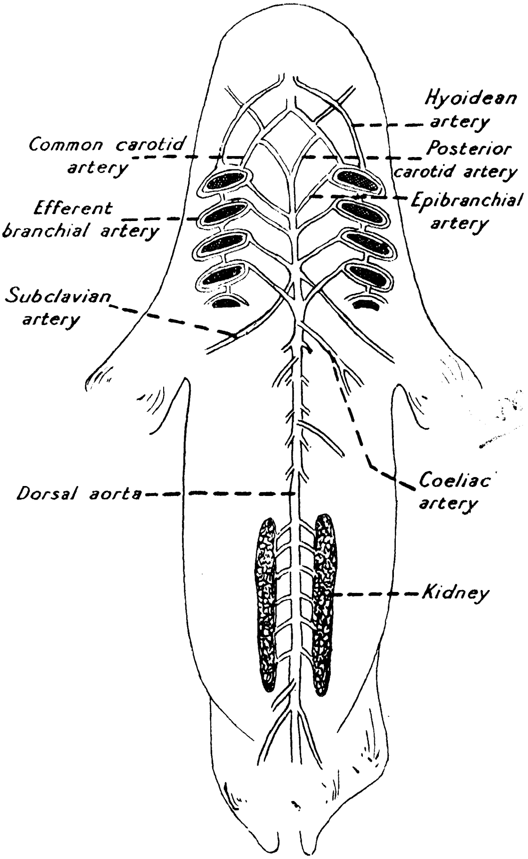


FIG. 81.—*Scyllium.* Efferent arterial system.

the roof of the pharynx, where these four pairs of arteries unite to form a **dorsal aorta.** This passes forwards and divides to form two small **posterior carotid** arteries, each uniting with the **common carotid** artery of its own side. Close to the origin of the first epibranchial artery from the corresponding efferent branchial artery there arises on each side a common carotid artery. This passes forwards beneath the skull and becomes subdivided into an external and internal branch, the former running forwards to the upper jaw and the latter penetrating the cranium to supply the brain. The **hyoidean** artery arises from the most anterior efferent branchial artery and supplies the pseudobranch of the spiracle before joining the internal carotid artery. Posteriorly the dorsal aorta extends throughout the whole length of the body, giving off a pair of **subclavian** arteries to the pectoral fins just before it receives the last pair of epibranchial arteries. Farther back it gives off a number of median vessels to the viscera, including (from in front backwards) a **cœliac, anterior mesenteric,** a **lieno-gastric,** paired **renals,** a **posterior mesenteric** and an **iliac,** whilst it is continued into the tail in the form of a **caudal** artery.

(B) VENOUS SYSTEM. The veins of the dogfish are mostly peculiarly enlarged to form sinuses. Of these the principal ones are the **anterior** and **posterior cardinal** and the **hepatic sinuses.** Blood from the liver is returned direct to the sinus venosus by a pair of spacious hepatic sinuses. The anterior region of the body is drained of blood by the anterior cardinal sinuses and a pair of small **inferior jugular sinuses.** Each anterior cardinal sinus is continuous in front with an **orbital sinus** around the eye, and this, in its turn, is in connexion with a **nasal sinus.** The anterior cardinal sinus communicates with the inferior jugular sinus by a short **hyoidean sinus,** whilst into the base of the anterior cardinal sinus runs a **subclavian sinus** from the pectoral fin. Each anterior cardinal sinus is continuous behind with a posterior cardinal sinus. This drains blood from the viscera, including the kidney of its own side. In the body-wall on each side runs a **lateral sinus,** returning blood eventually to the sinus venosus. All four sinuses—the anterior and posterior cardinals, the inferior jugular and the lateral—of each side unite outside the cœlom, and blood is conveyed from each to the sinus venosus by a **ductus Cuvieri,** which runs across the cœlom, as in *Amphioxus*. Blood is returned from the gut to the liver by an **hepatic portal** vein. A portal vein is one which terminates at both ends in the form of capillaries. Thus in the present case capillaries in the wall of the gut become united to form the hepatic portal vein, which itself breaks up into capillaries again in the liver. There is also a **renal portal system,** for blood from the tail is collected up into a caudal vein which forks, one branch going to each kidney, in the tissues of which it breaks up again, before being carried forwards by a posterior cardinal sinus.

The heart of the dogfish is described as "venous." This is on account of the fact that only once in the journey round the body does the blood reach the heart. From here it is passed to the gills for oxygenation, and on leaving them it is distributed direct to various organs of the body without being first returned to the heart, as in higher forms. Thus the heart contains nothing but de-oxygenated blood and is therefore described as venous. After leaving the heart the blood must pass through at least two sets of capillaries—i.e. those of the gills and then of some other organ—before being returned. Should it get into the hepatic portal or renal portal vein it will have to pass through three sets of capillaries in all.

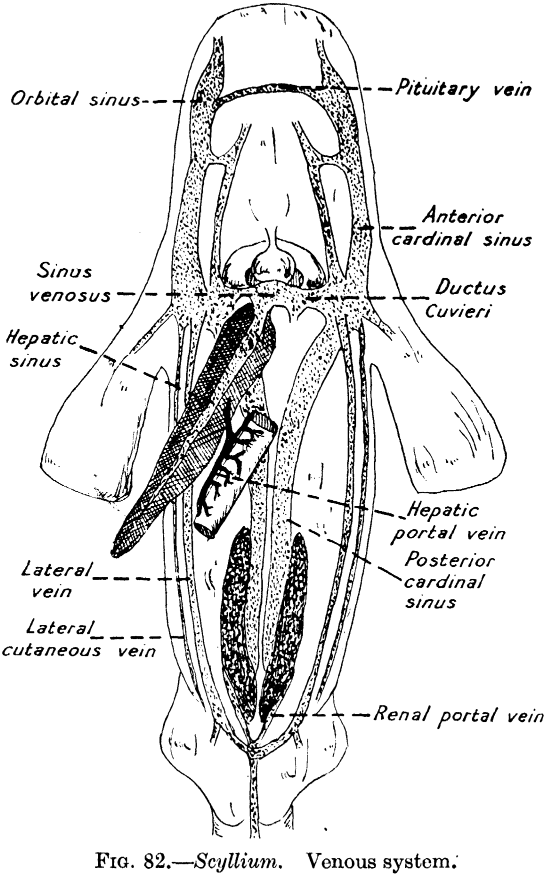


FIG. 82.—*Scyllium.* Venous system.

The Cœlom. The cœlomic cavity of the dogfish is divided into two regions by a septum. The anterior is a small pericardium enclosing the heart, whilst the remainder of the viscera lie in the posterior peritoneal cavity. The two are in communication by a small **pericardio-peritoneal canal** just below the œsophagus. To the anterior wall of the peritoneum is attached the liver by a falciform ligament, whilst a fold in the cœlomic epithelium carries the hepatic artery and the hepatic portal vein ; it is known as the **omentum.**

Nervous System. The nervous system is divisible into two distinct regions. The central nervous system consists of brain and spinal cord, whilst the peripheral nervous system is made up of a number of pairs of cranial and spinal nerves supplying respectively the two parts of the central nervous system.

(A) BRAIN. The brain is clearly divisible into fore-brain, mid-brain and hind-brain, whilst the fore- and hind-brains themselves are further divided each into two regions. Thus there are five parts in all to the brain, named from in front backwards the **telencephalon,** the **diencephalon,** the **mesencephalon,** the **metencephalon** and the **myelencephalon.** The structure of each region will be considered in turn. The telencephalon is laterally expanded to receive the olfactory lobes, whilst it itself is known as the cerebrum. In the floor of this region is the **optic chiasma,** in which the optic nerves from the eyes cross before entering the brain.

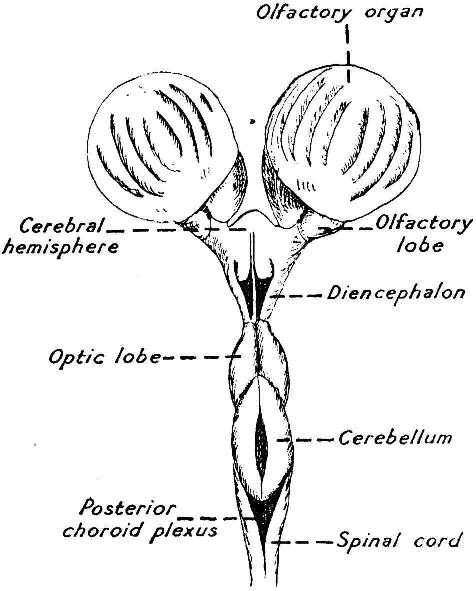


FIG. 83.—*Scyllium.* Dorsal view of brain.

The sides of the diencephalon are thickened to form the **optic thalami,** whilst from the floor arises a ventral outpushing known as the **infundibulum,** to which the pituitary body is attached. In a similar position on the dorsal wall arises the **pineal stalk.**

The roof of the mesencephalon bears a pair of thickened processes—the **optic lobes.**

The wall of almost the entire metencephalon has become thickened to form the **cerebellum,** whilst the thin-walled myelencephalon constitutes the **medulla,** passing insensibly back into the spinal cord.

Like the spinal cord itself the brain is tubular. The cavity of the fore-brain is known as the **third ventricle,** that of the hind brain as the **fourth ventricle,** and that of the mid-brain between them is narrow and is called the **aqueduct of Sylvius.** The whole brain is enclosed in a richly-vascularised membrane, known as the **pia mater,** which becomes much folded into the grooves of the third and fourth ventricles to form respectively an anterior and posterior choroid plexus. Outside the pia mater occurs a harder and more protective membrane, known as the **dura mater.** In the brain the grey matter (nerve cells) lies outside the white matter (nerve fibres) except in the cerebellum and optic lobes, where some of the nerve cells are superficial. In the spinal cord the white matter almost completely encloses the grey matter.

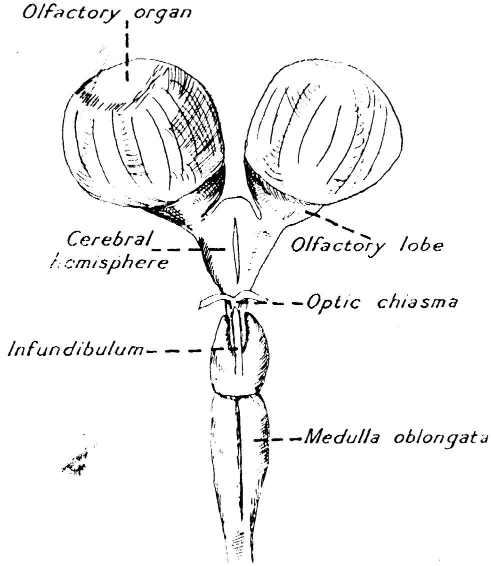


FIG. 84.—*Scyllium.* Ventral view of brain.

(B) SPINAL CORD. The spinal cord arises from the hind end of the medulla and passes dorsally along the whole length of the animal, being enclosed in the cavity of the vertebral column. It is covered by two membranous coats, similar to those of the brain, whilst it is hollow and its cavity, continuous with that of the brain, is filled with **cerebro-spinal fluid.**

(C) CRANIAL NERVES. From the brain of the dogfish there arise ten pairs of cranial nerves, concerned principally with the innervation of the head, though the posterior ones are not confined to that region. Their distribution is of great importance, and they will be dealt with individually. The first nerve, referred to as No. 1, and called the **olfactory,** is not a true nerve at all. It is formed actually by the elongation of certain sensory cells of the nasal epithelium. These penetrate the fore-brain, but the cell-bodies remain in the epithelium. Thus this pair of nerves resembles in origin the nerves of *Amphioxus.* Similarly, nerve No. II, known as the **optic,** is formed merely as an extension on either side of the

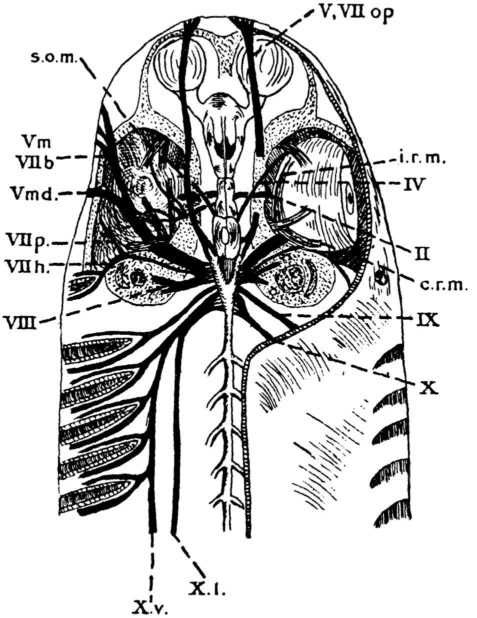


FIG. 85.—*Scyllium.* Cranial nerves.

b = buccal branch; e.r.m. = external rectus eye-muscle; h. = hyoid branch; i.r.m. = internal rectus eye-muscle; l. = lateral line; m = maxillary; md. = mandibular; op = ophthalmic branch; p = palatine branch; s.o.m. = superior oblique eye-muscle; v = visceral branch; II–X = cranial nerves.

brain itself. It is important to notice that these nerves, emerging from the floor of the diencephalon, cross before leaving the skull through the optic foramen of the opposite side to supply the eye-ball. The region where this crossing occurs is known as the **optic chiasma.** At this point it is essential that the muscles by which the eye is rotated in the orbit be described, for nerves III, IV and VI are concerned with their innervation. Attached to each eye there are six muscles, connecting it with the wall of the orbit. Four of them are known as **recti** muscles, and they all arise close together near the hind margin of the orbit, subsequently diverging to become inserted at various points into the eye-ball. The **superior rectus** and **inferior rectus** are inserted into the upper and lower side of the eye respectively, whilst the **internal rectus** runs forward behind the eye to be attached anteriorly. The **external rectus** is the shortest of them all and is inserted into the posterior margin of the eye-ball. Near the anterior end of the orbit arise two **oblique** muscles. The **superior oblique** runs on to the dorsal surface of the eye and its insertion occupies a position just anterior to that of the superior rectus. The **inferior oblique** muscle occupies a corresponding position in relation to the inferior rectus. Cranial nerve No. III is known as the **occulo-motor,** and supplies the superior, inferior and internal recti and the inferior oblique eye muscles. It arises from the ventral surface of the mesencephalon. No. IV is the **trochlear,** and is a slender nerve arising from the dorsal surface of the brain in the depression between the optic lobes and the cerebellum. It innervates the superior oblique muscle, whilst the external rectus is supplied by No. VI, a slender nerve arising from the ventral surface of the myelencephalon or medulla, and known as the **abducens.** The fifth cranial nerve is the **trigeminal,** so called on account of its division into three branches. It arises from the under surface of the myelencephalon, and almost at once a **superficial ophthalmic** branch leaves the rest of the nerve to run forwards within the cranium before emerging by a foramen to supply the skin of the snout region. The remaining two branches run together across the floor of the orbit to become divided eventually into a **maxillary** branch to the upper jaw and a **mandibular** to the lower. Just after its emergence from the skull this nerve becomes enlarged to form the **Gasserian ganglion.** Cranial nerve No. VII (the **facial**) also arises from the ventral surface of the myelencephalon, and has a complicated distribution. A **superficial ophthalmic** branch runs forwards over the eye in company with the similar branch of the trigeminal and innervates the lateral line organs of the head. A **buccal** branch passes forwards beneath the eye to supply the lateral line organs of that region, having crossed the orbit with the main branch of the trigeminal. The **palatine** branch also crosses the floor of the orbit, but posterior to the trigeminal, innervating the roof of the mouth. A large, **hyomandibular** branch runs across the hind wall of the orbit into the hyoid arch. The bulk of this nerve then passes posterior to the spiracle as a **postspiracular** branch, but it gives off a small **prespiracular** branch in front of the spiracle. It supplies the lateral line organs of the lower jaw, as described later. The eighth cranial nerve is the **auditory,** concerned with the innervation of the internal ear. It is to be regarded as a specialised branch of the facial nerve (No. VII). No. IX is the **glosso-pharyngeal,** arising ventro-laterally from the myelencephalon. It supplies the lateral line of its region and a **pharyngeal** branch passes to the gut. The bulk of the nerve runs behind the first gill-slit, first giving off a **pretrematic** branch in front of it. The **vagus** nerve, No. X, is the largest and arises by several roots just behind the glosso-pharyngeal. It emerges from the posterior end of the skull to run close to the anterior cardinal sinus of its own side. Soon after leaving the skull it gives off a branch to the lateral line, whilst it further supplies

Nerve	Name	Distribution
I	Olfactory	The nasal epithelium
II	Optic	The eye
III	Occulo-motor	All eye muscles except superior oblique and external rectus
IV	Trochlear	Superior oblique eye muscle
V	Trigeminal	
	(*a*) Superficial ophthalmic	Skin of the snout
	(*b*) Maxillary	The upper jaw
	(*c*) Mandibular	The lower jaw
VI	Abducens	External rectus eye muscle
VII	Facial	
	(*a*) Superficial ophthalmic	Lateral line above the orbit
	(*b*) Buccal	Lateral line below the orbit
	(*c*) Hyomandibular	Hyoid arch and lateral line of lower jaw
	(*d*) Palatine	Roof of the mouth
VIII	Auditory	The ear
IX	Glosso-pharyngeal	Pharynx and first branchial arch
X	Vagus	Second to fifth branchial arches, viscera and lateral line

a pre- and post-trematic branch to each of the remaining four gill-slits. After giving off these branches it passes posteriorly to innervate the heart and stomach.

The distribution of the cranial nerves may best be summarised by means of a table (see page 124).

The cranial nerves are of the utmost importance in elucidating the segmentation of the head. A discussion of this phenomenon will therefore be reserved until the distribution of the cranial nerves in other types has been described, and will be found in Chapter XXIII.

(D) SPINAL NERVES. In every segment behind the ninth (inclusive) there is a pair of fully-formed spinal nerves emerging from the spinal cord. Each consists essentially of two parts—a **dorsal root** bearing a ganglion and arising from the dorso-lateral corner of the spinal cord, and a **ventral root** arising from the ventro-lateral region. These two roots become united almost at once, but soon separate again into a **ramus dorsalis,** supplying the sensory structures, and a **ramus ventralis,** innervating the musculature of each segment. A **ramus communicans** connects each spinal nerve with a slender **sympathetic nerve-cord,** running up on either side of the dorsal aorta. As is usual in the Gnathostomata all the nerve fibres are medullated (page 167) except those of the sympathetic nervous system.

(E) LATERAL LINE. At intervals over the body of the dogfish are sense organs, known as **neuromast** organs. Each consists essentially of sensory, epidermal cells, bearing stiff hairs, and it probably functions to receive low-frequency vibrations. These sense organs are situated in canals, which have a well-defined distribution over the body and open to the exterior at intervals. Such a system of sense organs occurs only in fish and a few newts. One of these canals runs laterally along the entire length of the body, and is known as the lateral-line canal. The remaining canals may be considered as branches of it. Just in front of the level of the first true gill-slit each lateral-line canal gives off a transverse **occipital** canal, which runs up on to the dorsal surface of the head, where the two unite. The lateral-line canal itself continues forwards over the spiracle as a **temporal** canal, and this divides to form a **supra-** and **infra-orbital** canal, passing respectively above and below the eye. In addition there is an **hyoid** canal running ventrally behind the spiracle and turning forwards as a **mandibular** canal in the lower jaw. These last two canals are not well developed in the dogfish. In close association with the lateral-line canals are small sense organs, sunk into pits and known as the **ampullæ of Lorenzini.** The ear is one such organ, very highly specialised, and its structure will now be considered.

(F) EAR. This is essentially a pit which has become sunk in from the ectoderm, and is thrown at its inner end into a number of inter-communicating folds, whilst it retains its connexion with the exterior by a narrow tube, known as the **ductus endolymphaticus.** At the base this duct becomes enlarged and constricted to form two sacs—a dorsal **utriculus,** and a ventral **sacculus** opening into it. Communicating with the sacculus are three semi-circular canals, known respectively as the anterior, posterior and lateral, the first two lying vertical and at right-angles to each other, whilst the lateral canal is horizontal in position. Each canal ends in an ampulla, formed by a process of dilatation, and this contains an organ of balance. This is constituted by a number of sensory hairs, on which rest small, calcareous bodies, equilibrium being established when these are evenly distributed. Each ear is enclosed in an auditory capsule on its own side, the roof of this capsule being penetrated by the ductus endolymphaticus. The eyes of the dogfish essentially resemble those of the frog, described in Chapter XIV.

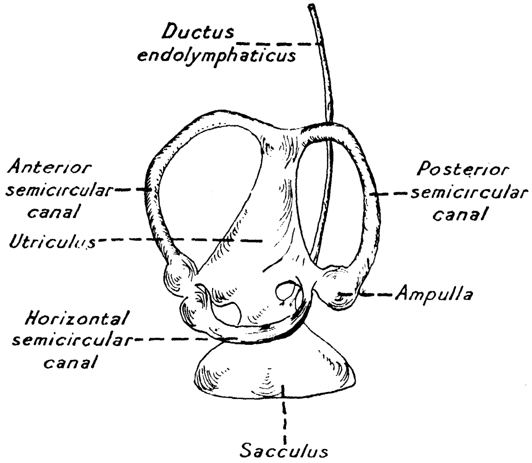

Ductus endolymphaticus
Anterior semicircular canal
Utriculus
Horizontal semicircular canal
Posterior semicircular canal
Ampulla
Sacculus

FIG. 86.—*Scyllium.* Ear.

(G) OLFACTORY ORGANS. These are particularly well developed in the dogfish, for they afford its principal means of guidance when in search of food. There is a pair of olfactory organs situated in the anterior end of the head. Each is a sac-like organ enclosed in an olfactory capsule. Its lining is thrown into a number of vertical folds, thereby increasing the surface, and the epithelium is highly sensitive. Each organ opens to the exterior by a nostril, but, unlike higher forms, the nasal chamber is not in communication with the mouth.

Urino-genital System. This system, as in the frog, is responsible for the elimination of liquid waste matter, as well as for the production and liberation of germ-cells, but since to some extent the same organs are employed, the system is treated as one composite whole. Though a fuller account of kidney structure is given in

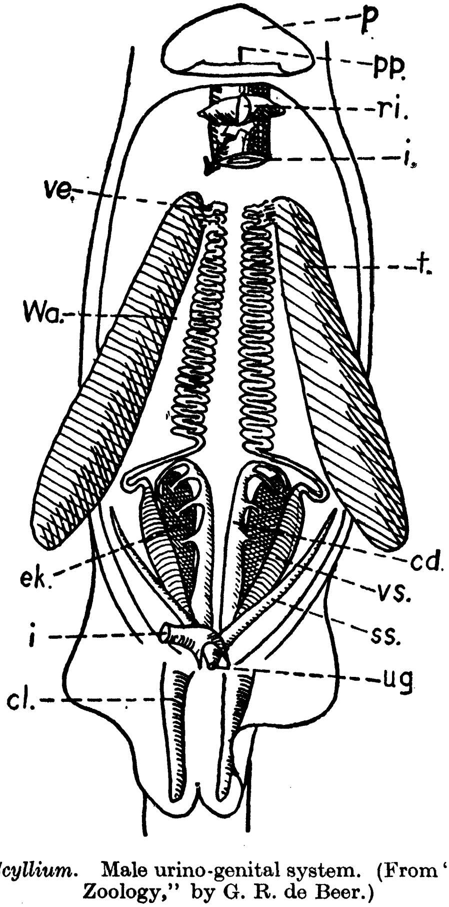


FIG. 87.—*Scyllium.* Male urino-genital system. (From "Vertebrate Zoology," by G. R. de Beer.)

cd., collecting duct; *cl.*, clasper; *ek.*, excretory portion of mesonephros; *i.*, alimentary canal cut; *p*, pericardium; *pp.*, pericardio-peritoneal canal indicated by an arrow; *ri.*, rudimentary opening of Müllerian ducts; *ss.*, sperm sacs; *t.*, testis; *ug*, urino-genital papilla; *ve.*, vasa efferentia; *vs.*, vesicula seminalis; *Wa.*, Wolffian duct.

Chapter XXII, it is essential at this point to give a brief indication of the early development of the kidney in the dogfish. In an early stage it consists of tubules, which are at first segmental in arrangement, opening at one end by **nephrotomes** into the cœlom and at the other joining a duct which leads to the exterior. The kidney is typically transversely divisible into three regions—**pro-, meso-** and **meta-nephros,** named from in front backwards. The pronephros quickly disappears, and it is the middle region (the mesonephros) which becomes the functional kidney of the adult *Scyllium*. The metanephros is not represented. Waste matter is eliminated through a long, mesonephric or **Wolffian duct,** which extends ventrally along the whole mesonephros. Active excretion is effected only by the posterior region of the mesonephros, the anterior portion disappearing, though the duct of this region remains in the male to form the vas deferens for the conveyance of spermatozoa to the exterior. Although the pronephros disappears its original duct on each side remains. Opening into the cœlom by the conjoined openings of the degenerated pronephric tubules there is found on each side in the female a duct, known as the **Müllerian duct,** and functioning as an oviduct. The Wolffian duct in both sexes opens into the cloaca on a median papilla, through which its products are shed. There is no urinary bladder in *Scyllium*.

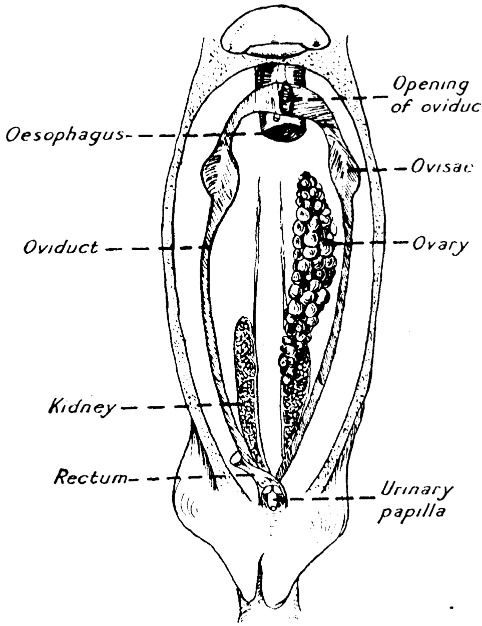
(A) MALE. There is a pair of large **testes** attached to the dorsal wall of the cœlom. Spermatozoa are conveyed away from each to the anterior end of the corresponding mesonephros by a number of fine tubules, known as the **vasa efferentia,** these being actually the original kidney tubules of that region. Thus the sperms are carried to the Wolffian duct, which itself becomes very much coiled, and is frequently known as the **vas deferens.** This becomes swollen at its posterior end to form a **vesicula seminalis,** where sperms are stored. The excretory products from the posterior portion of the mesonephros are passed into a collecting duct, which unites with the Wolffian duct. These conjoined tubes then open into a **sperm sac,** and the sperm sacs of the two sides become united to form a **urino-genital sinus,** itself opening into the cloaca on a **urino-genital papilla.**

(B) FEMALE. There is present an **ovary** on the right side only, attached, like the testes, to the dorsal wall of the cœlom. Eggs, when ripe, are shed into the cœlomic cavity, from which their only means of escape is the Müllerian ducts. These open funnelwise on the ventral side of the œsophagus, and pass uninterrupted to the cloaca. Some short distance behind their openings near the œsophagus a swelling on each marks the position of the **oviducal**

gland, where the material for egg-cases is secreted. Thus in the female the mesonephros plays no part in the evacuation of genital products. It is purely excretory, and the Wolffian ducts each become swollen posteriorly to form an **urinary sinus,** opening by a median, urinary papilla into the cloaca.

It is of importance to notice that the Müllerian ducts are represented in the male merely by a pair of vestigial funnels on the ventral side of the œsophagus and by the sperm sacs.

Sperm is transferred from the male to the female by the aid of the claspers of the former. Fertilisation is internal, after which the egg-cases harden and are liberated. Each is drawn out at several points into filamentous processes, by means of which attachment to sea-weed is effected. The egg in this condition is known as a "Mermaid's purse," and early development of the embryo takes place within it.



V. good.

FIG. 88.—*Scyllium.* Female urino-genital system. The ovary has been displaced to the left side.

Ductless Glands. These structures are described more fully in Chapter XXIX, but it may be as well at this stage to indicate to what extent they are represented in the dogfish.

As a result of the loss of the ciliary mode of feeding, as encountered in *Amphioxus*, two organs have been enabled to become specialised in other directions, whilst before they were used to accommodate this method of feeding. Thus the wheel-organ of *Amphioxus* is represented by an ectodermal inpushing from the roof of the mouth, forming the **hypophysis,** which becomes intimately connected with a downgrowth from the floor of the diencephalon—the **infundibulum** —to form the **pituitary body.**

The endostyle has become sunk beneath the floor of the mouth and completely closed off to form the **thyroid** gland. In some dogfish it still bears a number of cilia.

In *Amphioxus* the original, segmental gill-slits become much subdivided by means of the tongue-bars, growing down from the roof of the primary gill-slits. These are not present as such in *Scyllium,* but a number of glandular masses from the roofs of the gill-slits, situated in close association with the anterior cardinal sinus of each side, form a **thymus** gland.

Between the posterior ends of the kidneys, arising from the cœlomic epithelium, is a structure known as the **inter-renal** body, whilst lying at intervals along the sympathetic nerve-chain is a mass of tissue of nervous origin. Each of these is a **supra-renal** body.

The Class Pisces. In conclusion a few points may be made concerning the diagnostic features and classification of the class Pisces. Members of this class are cold-blooded—that is their blood is always at the temperature of the environment. They are, of course, Chordata, having a vertebral column, and possess both paired and median fins. The body is covered by an armour of denticles or placoid scales, one of the chief functions of which is to ward off attacks by ectoparasites. The gill-slits, which are a feature of all the Chordata, persist throughout life, whilst lungs are only occasionally developed. During development no amnion or allantois (embryonic membranes) are formed. This class is further subdivided by making use of certain well-defined criteria. Thus the Chondricthyes consist of forms whose skeleton is cartilaginous, whilst those with a skeleton of bone comprise the Osteichthyes. Important amongst these latter are the Dipnoi. There are only three genera existing to-day, and arising from the œsophagus is a paired outgrowth, giving rise to an air-bladder. This structure is highly important as a respiratory organ in the Dipnoi, for the fresh-water streams in which they live frequently dry up in the summer. Accordingly, the blood-circulation is considerably modified. An air-bladder occurs in other Osteichthyes, but here it is degenerate and serves merely as an hydrostatic organ, enabling its possessors to maintain themselves at certain depths. In origin it resembles the Tetrapod lung, with which it is therefore said to be homologous. In spite of this curious development the Dipnoi are regarded as an evolutionary side-line and not as representing ancestral Tetrapod stock.

CHAPTER XIV

RANA TEMPORARIA

THE common frog, *Rana temporaria,* is found in damp grassland in Britain, usually in the vicinity of streams and ponds. In winter it undergoes a sort of hibernation, burying itself in the mud at the bottom of a pond, where it remains quiescent until the following spring.

External Features. The body of the frog is clearly divisible into head, trunk and limbs. There is no neck present, the head passing insensibly into the trunk. Locomotion is effected mainly by the hind limbs, which become specially strengthened in adaptation to the frog's hopping mode of progression. The skin is green in colour and of a mottled pattern. On the head may be seen a pair of bulging eyes, the upper lids of which are thick, opaque and almost immovable, whilst the lower lids, which can be drawn upwards across the eye, are thin and transparent. It is important to notice that this latter lid does not correspond to the lower eyelid of mammals, this being entirely absent in the frog. It is a third eyelid, represented in mammals by the **nictitating membrane,** situated in the inner corner of each eye. Just in front of each eye is a small nostril, whilst posterior to each eye is an ear-drum or **tympanum.** There is no external ear, or pinna, and in higher forms it will be observed that the tympanum itself has become sunk in beneath the surface of the head, thus affording protection to it. The fore- and hind-limbs are similar in structure, though the hinder ones are considerably larger. Each is typically divisible into three regions—the upper limb, the lower limb, and the hand or foot. The hand and foot are similarly divisible. There is a proximal wrist (carpus), a palm (metacarpus) and fingers in the hand, and corresponding ankle (tarsus), instep (metatarsus) and toes in the foot. The male frog may be distinguished from the female externally by the presence on the first finger of the former of a roughened thumb-pad, which assists in the process of copulation. Situated between the hind legs is a small, rounded aperture, known as the cloaca. Through this fæces (solid waste matter), urine, and eggs or sperm are shed. Such a common aperture is termed a cloaca in contradistinction to the anus of higher forms, through which only solid waste matter is voided. Thus in this respect male and female frogs show no external distinction.

Skin. The skin of the frog is always moist, owing to the production of mucus by glands occurring at intervals over the entire surface. This mucus is important for two reasons. The frog breathes a great deal through its general body-surface when on land, and exclusively by this means when in water. Thus when on land it is essential that the skin be kept moist so as to facilitate a rapid gaseous exchange. This phenomenon is encountered in the earthworm. Furthermore this mucus, on account of its unpleasant taste and slimy nature, may afford the frog some protection from its enemies. Contained in the skin is a large number of pigment-spots, each composed of a collection of pigment-cells. According to environmental conditions, these cells may become expanded or contracted and the animal thus become lighter or darker in colour. Wet, dark or cold conditions tend to induce expansion, whilst the opposite conditions cause contraction of the pigment-cells. In this way some sort of protection may be effected by a simulation by the frog of the shade of the environment. The whole skin is enclosed in a thin, horny covering, and this is shed at intervals and devoured by the frog. The skin lies loose over the body-wall beneath, from which it is separated by a number of **subcutaneous lymph sacs** (page 150). A more detailed description (histology) of the skin will be found on page 164.

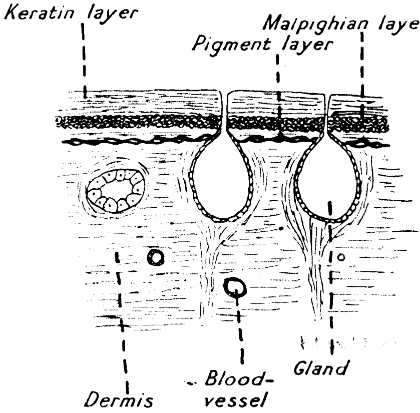


FIG. 89.—*Rana*. Skin.

Skeleton. The skeleton consists mainly of bone, but a certain amount of cartilage still remains. It is divisible into an axial skeleton, made up of skull and vertebral column, and an appendicular skeleton, composed of limbs and limb-girdles.

(A) SKULL. The skull is itself divided into a number of more or less distinct regions. Thus the brain is enclosed in a case, known as the cranium, to the anterior end of which is fused a pair of nasal capsules, and to the posterior end a pair of auditory capsules. Below the neurocranium (cranium plus capsules) occurs the visceral skeleton, highly developed in the dogfish, but in the frog repre-

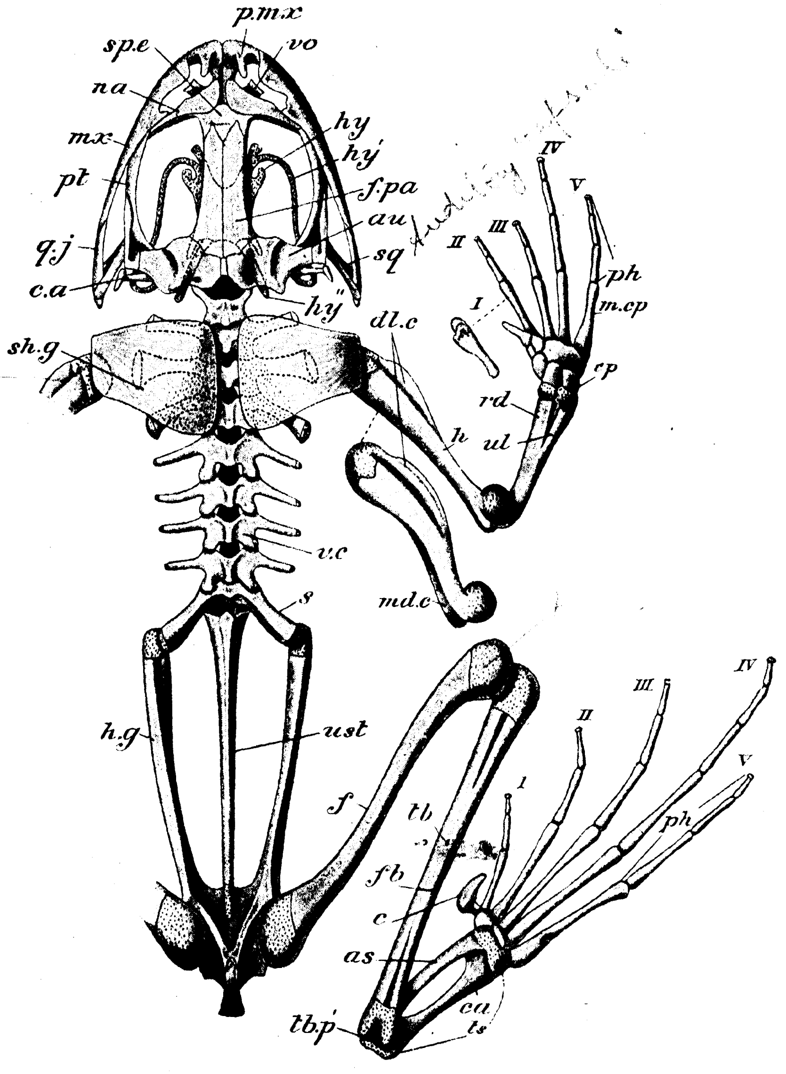


FIG. 90.—*Rana*. Skeleton, from the dorsal side. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

as, astragalus; *au*, auditory capsule; *c*, calcar; *c.a*, columella auris; *ca*, calcaneum; *cp*, carpus; *dl.c*, deltoid crest; *f*, femur; *fb*, fibula; *f.pa*, fronto-parietal; *h*, humerus; *h.g*, pelvic girdle; *hy*, hyoid, body; *hy'*, hyoid, anterior cornu; *hy''*, hyoid, posterior cornu; *m.cp*, metacarpals (metatarsals not specially lettered); *md.c*, medial crest; *mx*, maxilla; *na*, nasal; *ph*, phalanges; *p.mx*, premaxilla; *pt*, pterygoid; *q.j*, quadratojugal; *rd*, radius; *s*, sacrum; *sh.g*, pectoral girdle; *sp.e*, sphenethmoid; *sq*, squamosal; *tb*, tibia; *tb.p'*, tibio-tarsal joint; *ts*, tarsus; *ul*, ulna; *ust*, urostyle; *v.c*, vertebral column; *vo*, vomer; *I–V*, digits.

sented only by the skeleton of the jaws and by the hyoid apparatus in the floor of the mouth. The whole is so arranged as to enclose a pair of large orbits, into which the eyes fit. These differ from the orbits of higher forms in that the eye-balls of the frog are not separated from the cavity of the mouth by a layer of bone, but bulge backwards into it. The skull of the tadpole, from which that of the frog is developed, is cartilaginous, like that of *Scyllium.* Subsequently this becomes considerably strengthened by the formation of bones. Some of these actually replace the cartilage, and are known as cartilage-bones, whilst others are plastered on to the surface. These latter are called membrane-bones, on account of the fact that their position is previously indicated by the presence of connective-tissue membranes.

At its posterior end the skull is pierced by a large hole, known as the **foramen magnum,** through which passes the nerve-cord to establish continuity with the brain. The foramen magnum is bordered on each side by an **exoccipital** cartilage-bone and above and below by cartilage. At the anterior end is another cartilage-bone, the **sphenethmoid.** This is in the form of a box, narrowing towards its anterior end, near which a transverse partition separates the cranium from the cavity in front. The whole dorsal surface of the skull is covered by a pair of membrane-bones, the **fronto-parietals,** extending from the sphenethmoid to the exoccipitals, whilst along the ventral surface runs a dagger-shaped **parasphenoid,** the blade of which points in an anterior direction and the transverse portion of the hilt is extended to cover the floor of the auditory capsules.

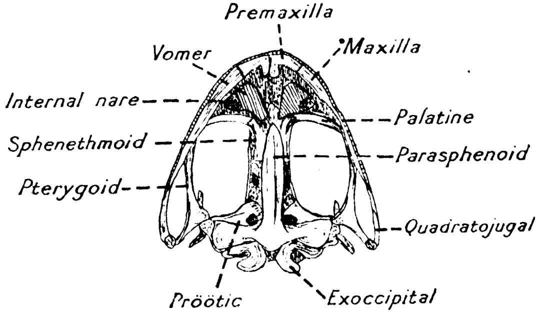


FIG. 91.—*Rana.* Ventral view of skull.

The nasal capsules are continuous with the front end of the cranium, and consist mostly of cartilage, except for the anterior extension of the sphenethmoid beyond the limit of the cranium. The cavity of the sphenethmoid in the nasal region becomes divided by a vertical partition, termed the **mesethmoid,** into right and left halves. Each capsule is open below and above, for the external nares (nostrils) each lead by a tube into the nasal capsule of its own side, whilst below a tube passes from the nasal capsule into the mouth, into which it opens by an internal nare. Covering the dorsal surface of each capsule is a membrane-bone, known as the **nasal,** whilst the floor of each is protected by another membrane-bone—the **vomer.** Embedded in this latter is the vomerine tooth of its own side.

Continuous with the postero-lateral corners of the cranium are the auditory capsules, consisting mostly of cartilage. Each contains a somewhat subdivided cavity, known as the **cartilaginous labyrinth,** in which is embedded the internal ear, described in contrast as the **membranous labyrinth.** The anterior portion of each auditory capsule becomes ossified to form the **proötic** (thus a cartilage-bone), and on to this is fixed a T-shaped membrane-bone, the **squamosal,** with the free limb of the T directed ventro-laterally. In order for communication to be established with the outside it is essential that at one point in each capsule cartilage should be absent. This region is known as the **fenestra ovalis,** and across it a membrane is tightly stretched. This is separated by a short space from the ear-drum, or tympanum, and thus a rod of bone must connect these two membranes in order that vibrations may be transferred from one to the other, and hence ultimately to the ear. This bone is the **columella auris.**

Since the brain and sense organs are thus enclosed within the neurocranium, it follows that apertures, known as foramina, must be pierced in the lateral walls, especially of the cranium, to permit the passage of nerves to and from the brain, as well as allowing a supply of blood to reach this organ. The skull of the frog is too small for a detailed study of the foramina to be made here, but they are dealt with in the case of the skulls of *Scyllium* and the dog.

The skeleton of the upper jaw consists essentially of an inner and outer series of paired bones. The **palatine,** a membrane-bone, is attached by a rod of cartilage to the hind end of the nasal capsules. To the posterior end of this cartilaginous rod, behind the palatine, is attached the foot of a Y-shaped **pterygoid,** with the arms of the Y directed backwards. The inner arm abuts on to the auditory capsule, whilst the outer runs ventro-laterally beneath and parallel to the long limb of the squamosal, from which it is separated by a rod of cartilage, known as the **quadrate,** and it is continuous at its inner end with the auditory capsule. The outer series of membrane-bones comprising the upper jaw are the **premaxillæ,** the **maxillæ** and the **quadratojugals.** The premaxillæ are a pair of small bones plastered on to the ends of the nasal capsules, the two meeting in front in the middle line. Behind the premaxilla on each side is a long, slender maxilla. Anteriorly this is expanded dorsally to abut on to the nasal capsule, which is thus provided with extra support, whilst posteriorly it is connected by another bone, the quadrato-jugal, with the quadrate. The premaxillæ and maxillæ each bear a single row of teeth.

The lower jaw consists of two rods, each termed a **Meckel's cartilage,** and these are joined in the front by a ligament. At the anterior end a small portion of each primitive, cartilaginous rod has become ossified to form a small cartilage-bone, the **mento-meckelian.** Plastered on to the outer surface is a **dentary** membrane-bone, whilst inside each Meckel's cartilage is almost completely covered by another membrane-bone, the **angulo-splenial.** Posteriorly each Meckel's cartilage articulates with the quadrate of its own side.

The remainder of the splanchnocranium (i.e. the skull other than the neurocranium) is constituted by the **hyoid** apparatus. This is a median plate, consisting almost entirely of cartilage, occurring in the floor of the mouth. The main bulk of this structure is termed the body. On each side of it there arise three pairs of short processes, directed backwards. At the anterior end are two very long processes, known as **cornua,** which, after running backwards for some distance parallel to the body, turn forwards and upwards to become attached to the sides of the auditory capsules. Two smaller posterior cornua project backwards, one on either side of the trachea (wind-pipe), and these are the only portions of the hyoid apparatus to become ossified.

The method of jaw-suspension in the frog is known as **autostylic,** the quadrate being directly attached to the neurocranium and the columella-auris (represented by the hyomandibula of *Scyllium*) playing no part in this suspension.

(B) VERTEBRAL COLUMN. This consists of nine rings of bone, known as vertebræ, placed together end to end so as to form a bony tube to contain the spinal cord. At the posterior end is a long, tubular bone, termed the **urostyle,** articulating with the ninth vertebra and consisting of a number of fused vertebræ. Each vertebra consists of a body or centrum, situated beneath the spinal cord and giving off a neural arch on either side to enclose this structure. Each centrum is concave in front and convex behind, except the eighth, which is concave at both ends. At the line of junction of the two neural arches is formed a neural spine in the form of a ridge, whilst on each arch except those of the first vertebra is developed laterally a pair of transverse processes. These are especially large in the sacral (ninth) vertebra, for these articulate with the dorsal ends of the ilia of the pelvic girdle. At the free end of each transverse process is a small pad of cartilage, representing a rib. The transverse processes provide means of attachment for muscles. At the front and hind ends of each vertebra are special articulating surfaces, known as **zygapophyses.** The anterior zygapophyses are directed upwards and slightly inwards, whilst the posterior zygapophyses face downwards and slightly outwards. The posterior zygapophyses of each vertebra articulate with the anterior zygapophyses of the vertebra next in front, elasticity thus being imparted to the vertebral column whilst a certain flexibility is allowed for. Between every two successive vertebræ there is enclosed on each side an intervertebral foramen, through which emerges a spinal nerve. One such pair of apertures occurs a short distance behind the front end of the urostyle for the egress of the tenth spinal nerves. The first vertebra is somewhat modified and is known as the **atlas.** It has no transverse processes, and articulates in front with the exoccipital condyles of the skull.

(C) PECTORAL GIRDLE AND FORE-LIMB. The pectoral girdle consists of an almost complete hoop of cartilage and bone, lying in the body-wall of the anterior region of the trunk and divisible into two identical halves in the midventral line, where these two halves unite in a symphysis. Like the corresponding structure in the dogfish, each half of the pectoral girdle is divisible into a dorsal scapular and a ventral coracoid region, but in the frog the original cartilage has become largely replaced by bone (therefore cartilage-bone), whilst there is one pair of membrane-bones developed, the **clavicles.** The most dorsal region consists of a large, broad plate on each side, known as the **suprascapula,** consisting almost entirely of calcified cartilage, except for a small region near its union with the scapula. Laterally the suprascapula is connected with a smaller cartilage-bone, the **scapula,** an anterior projection from which forms the **acromion process.** Ventral to the scapula lies the coracoid region, composed of cartilage and bone and attached laterally to the scapula. The **coracoid** bone itself is situated posteriorly and is separated from a slender membrane-bone, the clavicle, in front by a coracoid fontanelle. The clavicle itself extends forwards along the inner side of the acromion process. Lying along the clavicle and posterior to it is a strip of calcified cartilage, the **precoracoid,** whilst this is continued in a posterior direction to form the **epicoracoid** along the inner margin of the coracoid itself. The two halves of the girdle become continuous in the midventral line, a symphysis being established between the pre- and epicoracoids of the two sides. Posteriorly there is attached to the epicoracoids a median cartilage-bone, known as the **xiphisternum,** continuous with an expanded **xiphoid** cartilage. In front the fused precoracoids have attached to them a cartilage-bone, the **omosternum,** bearing on its free extremity a small plate of cartilage, called the **episternum.** Enclosed between the scapula and coracoid on each side is a depression. This is the **glenoid cavity,** into which fits the head of the first bone of the fore-limb.

The bone of the upper arm is the **humerus.** This is chiefly characterised by a **deltoid ridge** along its inner side, whilst the main shaft of the bone is swollen at each end. The proximal swelling forms the head, set in the glenoid cavity, whilst the distal swelling is known as the **trochlea,** and serves for the reception of the bone of the fore-arm. This latter is the **radio-ulna,** so called on account of its double nature, the radius and ulna being separate bones in mammals. The radial portion of this composite bone in the frog lies on the inner side of the limb, though twisting slightly to lie above the ulnar portion proximally. There is an heel-like process on the radio-ulna projecting backwards beyond the region of articulation with the humerus, and this is known as the elbow or **olecranon process.** The wrist or **carpus** is made up of a number of carpals, arranged in two rows. The proximal row consists of three carpals, named the **radiale, intermedium** and **ulnare,** whilst the distal row in the adult frog also contains three such bones, five being present in early stages of development and subsequent fusion taking place. There are only four fully-formed digits, each consisting of a basal metacarpal, articulating with a number of

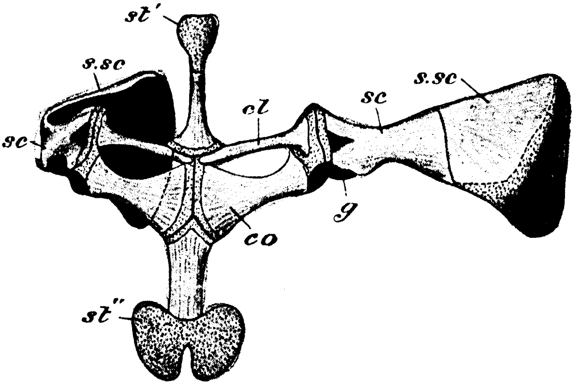


FIG. 92.—*Rana.* Pectoral girdle, from ventral side. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

cl, clavicle ; *co,* coracoid ; *g,* glenoid facet ; *sc,* scapula ; *s.sc,* suprascapula ; *st',* episternum ; *st'',* xiphoid cartilage.

phalanges. The first digit, known as the **pollex,** consists of a metacarpal only, whilst digits II, III, IV and V bear respectively two, two, three and three phalanges.

(D) PELVIC GIRDLE AND HIND-LIMB. This, like the pectoral girdle, is made up of two halves, fused together ventrally to form between them an almost complete hoop of bone. But, whereas the pectoral girdle was placed almost at right angles to the vertebral column, the pelvic girdle is so set as to lie almost parallel to it. On the outer side of each half is a cavity, known as the **acetabulum,** for the reception of the head of the bone of the thigh. Situated above this is the **ilium,** running forwards to become attached to the transverse process of the sacrum of its own side. The two ilia meet posteriorly and fuse to form an iliac symphysis. This iliac region corresponds to the scapular region of the pectoral girdle. The portion of the pelvic girdle lying below the acetabulum is termed the **ischio-pubic** region, and corresponds to the coracoid region of the pectoral girdle. It is made up of a cartilaginous **pubis,** forming the anterior portion of the girdle, thus corresponding to the precoracoid of the pectoral girdle. The two pubes become completely united in a pubic symphysis. The posterior part of this ventral portion is made up of the **ischium,** corresponding therefore to the coracoid proper. The two ischia also become completely fused. Between the pubis and ischium lies a piece of calcified cartilage, known as the **post-pubic cartilage.** This cartilage and the three bones mentioned all play a part in enclosing the acetabulum.

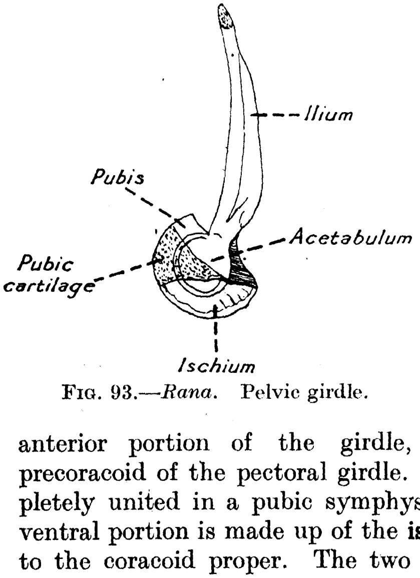


FIG. 93.—*Rana.* Pelvic girdle.

The thigh-bone, or **femur,** is long and very slightly curved. Proximally it fits into the acetabulum, and from this head end projects a small process known as the **trochanter.** The bone of the lower leg is the **tibio-fibula,** of double nature, as indicated by a groove running almost throughout its whole length. In many higher animals the two components of this bone are completely separated. In the frog the tibial portion is pre-axial in position, and the fibular portion post-axial. It is expanded at both ends, and its lower end articulates with the ankle or **tarsus.** There are only two proximal tarsals, the astragulus (on the tibial side) and the calcaneum (on the fibular side). These are widely separated in the middle, but united at both ends. There are only two small distal tarsals, articulating with six metatarsals, which form the instep, and with which the phalanges of the toes articulate. On the inner side of the first toe, or **hallux,** lies a small toe, the **calcar,** consisting of a short metatarsal and two phalanges, the hallux itself also bearing two phalanges. Digits III to VI (counting the calcar as II) possess respectively two, three, five and three phalanges.

Internal Anatomy. Though all the internal organs of the frog function as one collective whole to effect its life-processes it is convenient for purposes of description to segregate them into a number of groups. All the organs included in each such group are concerned primarily with some one particular function, and together they comprise a system. The various systems of the frog will therefore be dealt with in detail individually.

Alimentary System. The alimentary system consists of a tube leading from mouth to anus and through which all the food passes. It is considerably longer than the body of the frog, and is therefore coiled. Arising from and functioning in conjunction with this tube is a number of other organs which will therefore be included in a description of the alimentary system. In the mouth or buccal cavity of the frog is contained a long, coiled tongue. This is peculiar in that it is attached at the front of the mouth, and when at rest is rolled up within it. It is forked and sticky at the tip, and may be shot out rapidly to effect the capture of an insect on which the frog feeds. The frog's food is not confined to insects, for it includes earthworms, slugs and other " grubs " in its diet. The upper jaw is fringed by a single row of teeth. Each of these is a conical structure, closely resembling the placoid scales of the dogfish. It consists of an hollow mass of **dentine,** covered by a cap of **enamel.** Into the dentine extends a vascularised **pulp-cavity.** As these teeth wear out they are replaced by new ones. On the roof of the mouth is a pair of rough vomerine teeth, to the outer side of each of which

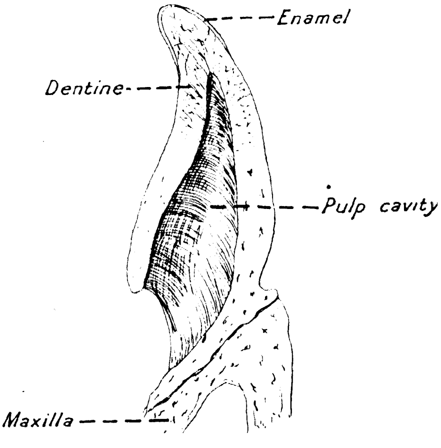


Fig. 94.—*Rana.* Vertical section of teeth.

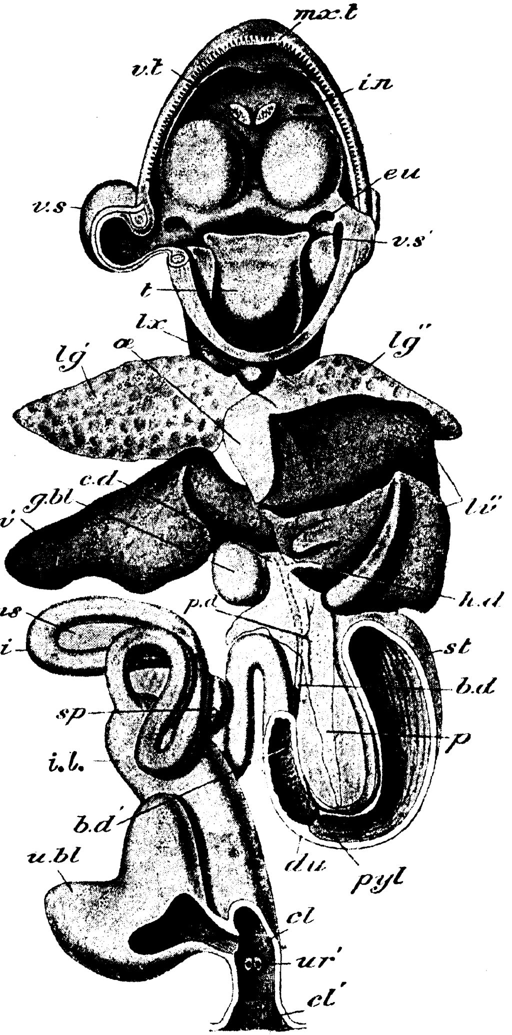
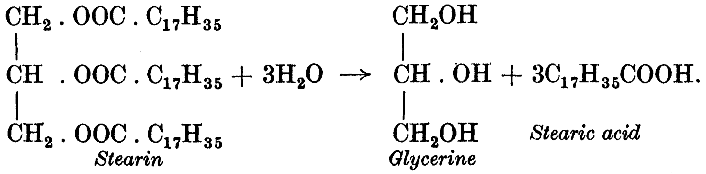


FIG. 95.—*Rana*. Alimentary canal and its diverticula.

b.d, so-called bile duct; *b.d'*, aperture of same; *c.d*, cystic duct; *cl*, cloaca; *cl'*, aperture of same; *du*, duodenum; *eu*, Eustachian aperture; *g.bl*, gall bladder; *h.d*, hepatic duct; *i*, intestine; *i.l.*, rectum; *i.n*, internal nare; *lg'*, right lung; *lg''*, left lung; *lv'*, liver, right lobe; *lv''*, liver, left lobe; *lx*, larynx; *ms*, mesentery; *mx.t*, premaxillo-maxillary teeth; *p*, pancreas; *p.d*, pancreatic duct; *pyl*, pylorus; *sp*, spleen; *st*, stomach; *t*, tongue; *u.bl*, bladder; *ur'*, aperture of ureter; *v.s*, right vocal sac; *v.s'*, orifice of left vocal sac; *v.t*, vomerine tooth.

opens an internal nare. The posterior extremity of the mouth is known as the pharynx, and into it opens a pair of **Eustachian tubes,** communicating with the inner side of each tympanum. In the male these Eustachian tubes are extended laterally to form the **vocal sacs,** which largely facilitate the croaking sound emitted principally in the breeding season. In the floor of the pharynx is a slit-like aperture, known as the **glottis,** which leads to the trachea or windpipe. During swallowing this glottis can be closed, and thus food is prevented from passing into the trachea. From the pharynx the alimentary canal is continued backwards in the form of a narrow **œsophagus.** This leads into a wider **stomach,** somewhat constricted at either end. At its distal end this constriction is known as the **pylorus,** and leads into a **duodenum.** The opening between the stomach and the duodenum can be closed by means of a sphincter muscle (see page 114). The duodenum is narrow and turns forwards so as to run parallel to the stomach. It leads into the still narrower, coiled **intestine,** which widens at its posterior end to form the **rectum.** This is short, and the alimentary canal now terminates by opening to the exterior as the **cloaca.** On to the ventral surface of the hind end of the rectum opens an urinary bladder. As well as the simple tube already described, a number of glands go to comprise the alimentary system. A gland is an organ concerned in the elaboration of some definite chemical substance. The largest of these glands is the **liver.** This is attached near the base of the œsophagus, and consists of a large left lobe, a slightly smaller right lobe and a small median lobe. Between the right and left lobes occurs a structure, usually green in colour, known as the **gall-bladder.** Leading from this to the duodenum is a narrow tube, known as the **bile-duct.** Though this is not easily seen in dissection it can often be observed by first squeezing the gall-bladder between the thumb and finger, when the green bile forced into this duct renders it more conspicuous. Between the stomach and the duodenum lies an elongated, yellowish gland, termed the **pancreas.** This is in connexion with the duodenum by way of the bile-duct, which traverses it.

It is now necessary to discover what happens to the food during its passage through the alimentary canal. Here it undergoes a process of digestion, by which the nutritious part of the food, as distinct from the waste, is brought into solution so that it can be absorbed into the blood for distribution to all parts of the body. This is effected by the treatment of the food with a number of chemical reagents, known collectively as digestive juices. Each of these contains one or more enzymes, functioning in the manner of an organic catalyst. These enzymes exist, therefore, only in small quantities and assist in various chemical reactions involved, rather than actually effecting them. It will be seen that two of the digestive juices do not contain enzymes. The food is not chewed in the mouth, but is swallowed whole. There is no saliva present in the mouth of the frog. Once in the stomach the food encounters **gastric juice.** This contains an enzyme, known as **pepsin.** It attacks proteins, converting them to the peptide stage. It will act only in acid solution, and this is provided by the hydrochloric acid produced, like the gastric juice itself, by the epithelium lining the stomach. It is of little digestive function in the frog, but it is sufficiently concentrated to kill any prey swallowed alive. When the concentration of the acid in the stomach reaches a given value the sphincter muscle becomes relaxed and the food passes into the duodenum. Here it encounters the **bile** and the **pancreatic juice.** The action of the bile is to emulsify fats, breaking them up into small globules as a result of the reduction of their surface-tension. Thus the surface of the fats is increased for the subsequent action of the pancreatic juice. The bile itself is partly an excretory product, for its green colour is due to the carriage of partly-decomposed hæmoglobin. It is alkaline, owing to the presence in it of sodium carbonate, and thus the action of the gastric juice is stopped. The pancreatic juice itself contains three enzymes. **Amylase** attacks starches and glycogen, converting them into maltose. **Lipase** converts fats into fatty acids and glycerine. The third pancreatic enzyme is called **trypsin,** but it is actually secreted in the form of an inactive precursor, known as **trypsinogen,** which becomes active only on meeting a further enzyme—**enterokinase**—in the intestine. In this active form trypsin converts peptides to amino-acids. It will be remembered that the bile is alkaline, sodium hydroxide being produced by the hydrolysis of the sodium carbonate present. Now this will, of course, combine with the fatty acids, liberated by the splitting up of the fats, to form the sodium salts of these fatty acids, these being soaps. The following example will make this clear. The fat known as stearin, common in lard, is broken up into stearic acid and glycerine. The stearic acid unites with the sodium hydroxide to form sodium stearate, which is a soap.



$$\begin{array}{lll} CH_2 \,.\, OOC \,.\, C_{17}H_{35} & & CH_2OH \\ | & & | \\ CH\ \,.\, OOC \,.\, C_{17}H_{35} + 3H_2O & \rightarrow & CH \,.\, OH + 3C_{17}H_{35}COOH. \\ | & & | \\ CH_2 \,.\, OOC \,.\, C_{17}H_{35} & & CH_2OH \qquad \textit{Stearic acid} \\ \quad \textit{Stearin} & & \textit{Glycerine} \end{array}$$

$$C_{17}H_{35}COOH + NaOH \rightarrow C_{17}H_{35}COONa + H_2O$$

Sodium stearate

The food now passes into the intestine, where it meets a final digestive juice, the **succus entericus.** The enzymes of the intestinal juice will be more fully discussed when the digestion of the rabbit is described (page 189). For the moment it is sufficient to realise that their action in the frog is essentially the same, for they function to complete the process of digestion. At this stage, therefore, the nutritious part of the food has all been converted into liquid form, and that which remains solid now is waste matter, which has resisted the action of the digestive juices. The liquid food is now absorbed into the wall of the intestine. To facilitate this process the wall of the intestine is considerably folded, each of the processes projecting into the lumen of the gut being known as a **villus.** Each of these contains an artery and a vein, united by a network of capillaries, as well as a lacteal vessel, connected with the lymphatic system (page 150), into which most of the fatty material is absorbed. Once within a villus the digested food is carried away in a vein, finally to reach the heart for distribution to various parts of the body. The waste matter is finally voided through the cloaca.

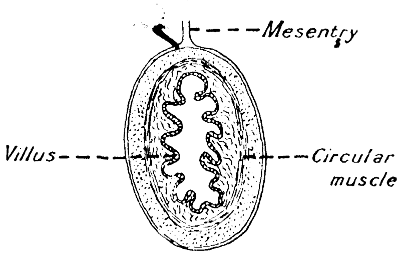


FIG. 96.—*Rana.* Section of intestine.

The passage of the food along the alimentary canal is brought about by a wave of muscular contraction, known as **peristalsis.** This is stimulated chiefly by the contact of the food with the wall of the gut, but in the intestinal region the soaps are of importance in this respect.

Vascular System. The main organ of the vascular system is the heart, acting as a pump to keep the blood in motion. The blood is conveyed about the body in vessels, known as arteries and veins. An **artery** is a vessel carrying blood away from the heart, whereas a **vein** carries it towards the heart. As will be seen later it is not true to say that an artery carries the " good " blood and a vein the " bad."

(A) HEART. The heart is divided into three chambers, known respectively as the **right** and **left auricles** and the **ventricle.** The latter is a thick-walled structure lying posterior to the two thinner and smaller auricles, the right of which is larger than the left. Lying on the dorsal side of the heart is a reservoir, known as the **sinus venosus,** into which is drained the de-oxygenated blood from all parts of the body. Lying ventrally across the face of the heart is a thick-walled, muscular tube, called the **truncus arteriosus.** This opens into the ventricle and provides the sole means of egress of blood from the heart. The whole heart is enclosed in a portion of the cœlom, walled off from the general peritoneal cavity and known as the **pericardium.** The openings between the various chambers of the heart and the vessels immediately connected with it are guarded by valves, formed by folds in the lining of the heart. Two small flaps of skin comprise the **sino-auricular** valves between the sinus venosus and the right auricle, into which it opens, whilst each auriculo-ventricular aperture is similarly guarded. These latter valves are held in position by fine cords, known as **chordæ tendinæ,** attached to the wall of the ventricle. There is no direct communication between the right and left auricles. Three small **semilunar** valves occur at the base of the truncus arteriosus, whereas near the top of this organ three more similar valves divide the truncus into a **conus arteriosus** (proximal) and a short **ventral aorta** (distal). Lying in the conus is a twisted **spiral valve.**

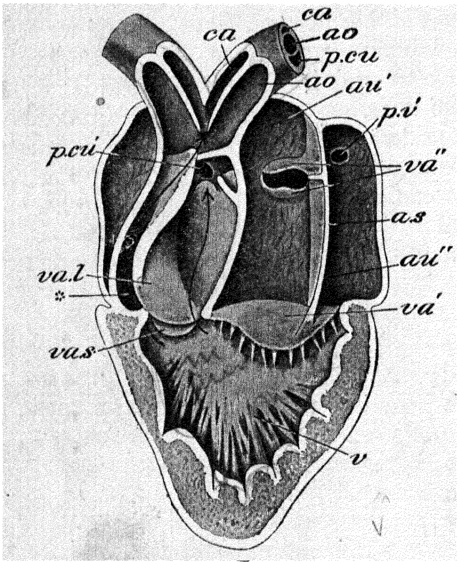


Fig. 97.—*Rana.* Heart, opened from ventral surface. (From "Atlas of Practical Elementary Zootomy," by G. B. Howes.)

a.s, interauricular septum; *ao*, systemic arch; *au'*, right auricle; *au''*, left auricle; *ca*, carotid arch; *p.cu*, pulmo-cutaneous arch; *p.cu'*, pulmo-cutaneous orifice; *p.v'*, orifice of pulmonary veins; *v*, ventricle; *va'*, dorsal auriculo-ventricular valve; *va''*, sinu-auricular valves; *va.l*, spiral valve of truncus; *va.s*, semilunar valve.

(B) Action of the Heart. Blood from the sinus venosus is conveyed to the right auricle, whereas the left auricle receives blood from the lungs *viâ* the pulmonary veins. Thus oxygenated blood lies in the left aurcile and de-oxygenated in the right. Both ventricles contract simultaneously, and their blood is forced into the ventricle, pure on the left, and impure on the right. These two lots of blood do not mix to any great extent for three reasons. First, the blood is in the ventricle only for a fraction of a second.

Second, the wall of the ventricle is spongy, and into the lumen of this chamber project muscular processes, known as **columnæ carnæ.** Third, blood itself is a fairly viscous liquid. Now the truncus opens from the right side of the ventricle, and forks at its distal end. Each of these branches becomes further divided into three arches, similar in arrangement on both sides. The posterior arches are the **pulmo-cutaneous,** along which blood is carried to the lungs and skin for oxygenation. The middle arches are the **systemics.** That from each side passes backwards, dorsal to the heart, and the two join just beneath the apex (tip) of the ventricle to form the dorsal aorta. Along the systemic arches blood is distributed to the trunk and limbs. The most anterior of the three arches turn forwards to supply the head. They are the **carotid** arches. When the ventricle contracts blood is forced up the truncus, de-oxygenated blood first. This passes along the pulmo-cutaneous arches to the lungs and skin, for pressure in this pair of arches is lower than in the other two, and therefore blood flows into them more readily. By this time the somewhat mixed and pure blood has reached the top of the truncus. But the pulmo-cutaneous arches are already filled with de-oxygenated blood, so that now blood flows into the systemic arches. When these are filled the pressure is no less in the carotid arches than elsewhere, so that the really pure blood passes to the head.

(C) ARTERIAL SYSTEM. The division of the truncus arteriosus has already been referred to. Shortly after its origin each pulmo-cutaneous arch divides to form a pulmonary artery to the lung of its own side and a cutaneous artery to the skin. From the outer side of each systemic arch during its passage backwards arises a **subclavian** artery to the fore-limb, whilst a number of important arteries is given off the dorsal aorta. Immediately behind the junction of the two systemic arches a **cœliaco-mesenteric** artery emerges from the ventral surface of the dorsal aorta to supply the gut. It becomes further subdivided into an **hepatic** (to the liver), a **cœliac** and an **anterior mesenteric,** supplying between them the spleen and the anterior part of the gut. Farther back a number of paired **renal** arteries runs to the kidneys, whilst a **spermatic** or **ovarian** artery arises in male and female respectively to supply each testis or ovary. Behind these a median **posterior mesenteric** artery arises to carry blood to the intestinal region. At its posterior end the dorsal aorta forks to form two **iliac** arteries, one running in either leg.

(D) VENOUS SYSTEM. Blood is returned from all parts of the body except the lungs by three great veins, opening into the sinus venosus. The three veins in question are the **posterior vena cava** and a **right** and **left anterior vena cava.** Each anterior vena cava becomes subdivided into three branches and each of these subsequently into two, making a total of six in all. These branches (from in front backwards) are the **lingual,** returning blood from the tongue, the **mandibular** from the lower jaw, the **internal jugular** from the brain, the **subscapular** from the shoulder region, the **brachial** from the arm and the **cutaneous** from the skin. The posterior vena cava is a median vessel lying in close association with the dorsal aorta. It receives two large **hepatic** branches from the liver, whilst posteriorly it terminates as a number of

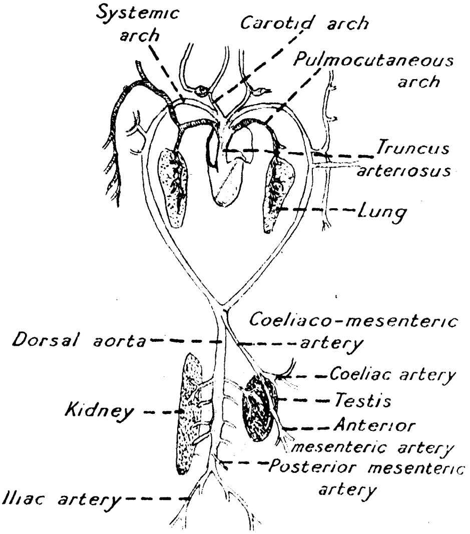


FIG. 98.—*Rana.* Arterial system.

paired **renal** veins, receiving blood from the kidneys, as well as the spermatics and ovarians from the reproductive organs of the male and female respectively. There are two important sets of vessels to be considered in connexion with the venous system of the frog, comprising respectively the hepatic portal and renal portal systems. A portal vein is defined on page 118. The **hepatic portal** vein is a single structure commencing as capillaries in the wall of the gut and terminating again in the form of capillaries in the tissues of the liver, where much of the carbohydrate material absorbed from the intestine is converted into glycogen and stored. There is a pair of **renal portal** veins, each of composite nature. Running from each hind leg is a **femoral** and **sciatic** vein. These unite at the base of the trunk to form a renal portal vein, passing up along the outer edge of the kidney of its own side and penetrating this organ to break up into capillaries. Arising from each femoral vein and passing antero-dorsally is a **pelvic** vein, running ventral to the sciatic of its own side. The pelvic veins unite in the midventral line in the body-wall and pass forwards as the **anterior abdominal** vein. When this reaches almost the level of the arms it leaves the body-wall and penetrates the liver, where it breaks up before continuing its journey to the heart, so that the anterior abdominal veins comprises part of the hepatic portal system.

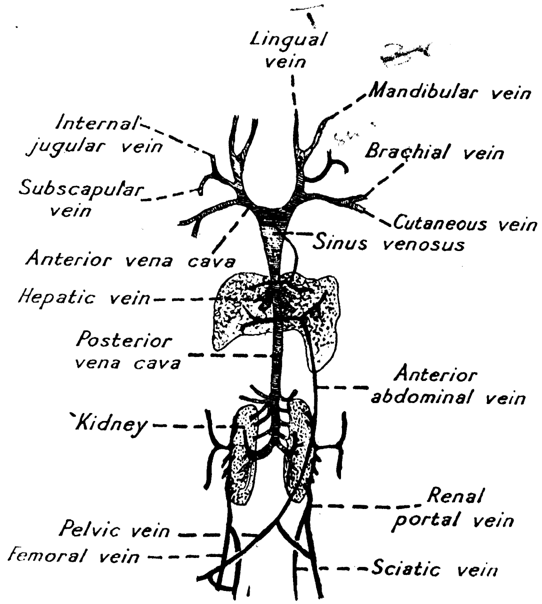


FIG. 99.—*Rana*. Venous system.

Blood is returned to the left auricle from the lungs by a pair of **pulmonary** veins, which unite to form a common vessel just before entering the heart.

(E) THE PRINCIPLE OF BLOOD-CIRCULATION. Every part of the body must be supplied with blood to facilitate both nutrition and respiration. It is therefore apparent that every such part of the body must be reached by a vein so that the blood, having given up its food and oxygen, may be conveyed away. When an artery reaches the organ it is destined to supply it fragments, the branches becoming progressively finer and more thin-walled until they eventually become designated as capillaries. From these the blood does not escape, but oxygen and liquid food diffuse outwards through the walls of the capillaries to supply the tissues. The actual capillaries of the arteries are continuous with those of the veins. These latter join one another to give rise to progressively larger vessels until eventually a vein running back to the heart, liver or kidney is formed. Thus the blood-system of the frog is described as closed, for the blood itself, including principally the red colouring matter, never escapes from the vessels in which it is carried, food and oxygen reaching the tissues by diffusion through the walls of the capillaries, when the blood thus exhausted is conveyed onwards, finally to reach the heart and be passed to the lungs or intestine for fresh supplies. This closed type blood-vascular system is characteristic of all the Chordata and many Invertebrata—e.g. the Annelida—and is to be contrasted with the open type found in Arthropods, where the tissues are actually bathed in blood.

The plan of blood-circulation in the frog is as follows. Oxygenated and de-oxygenated bloods leave the ventricle, the former to be supplied to the various organs of the body except the lungs and skin, which are supplied by the latter. Blood from the lungs is returned to the left auricle, whilst that from the remaining organs of the body reaches the right auricle through the sinus venosus. These facts may be summarised in Fig. 100.

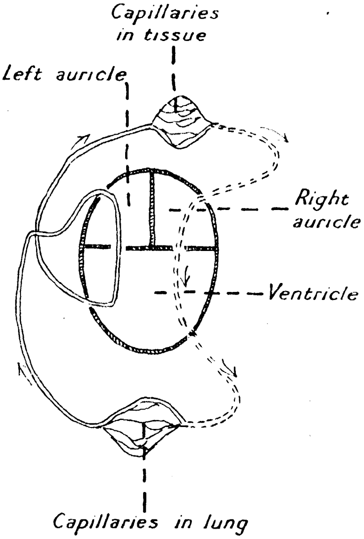


FIG. 100.—*Rana*. Diagram of blood-circulation.

Lymphatic System. It will be remembered that the tissues are bathed not in blood itself, but in a nutrient fluid which exudes through the walls of the capillaries. This fluid is known as **lymph.** It comes to lie in small **lymph-vessels,** several of which may join to form a **lymph-sac.** Some of these are contractile and are known as **lymph-hearts,** which pump the lymph back into the great veins of the body Thus there is one pair of lymph-hearts near the urostyle, opening into the femoral veins, whilst an anterior pair below the scapulæ communicate with the subscapular veins.

Respiratory System. It has already been pointed out that the frog uses its skin to a considerable extent for respiratory purposes. On this account it is kept moist to facilitate gaseous exchange when the animal is on land, whereas when it is in water it relies exclusively on the skin for effecting respiration. When on land the frog breathes very largely by means of a pair of lungs. Leading from the ventral side of the œsophagus is a **trachea,** or windpipe, forking very soon to form a pair of **bronchi,** one running to each lung. Within the lung each bronchus becomes expanded, whilst the internal surface is considerably increased by being thrown into a number of folds. The trachea itself consists almost entirely of **larynx,** or voice-box, supported by a **cricoid** and a pair of **arytenoid** cartilages. Inspiration (the taking in of air to the lungs) and expiration (the reverse process) are effected after the manner of a force-pump. Air is gulped into the mouth, when the mouth is tightly sealed and the nostrils closed. The hyoid apparatus in the floor of the mouth is then raised, and this results in air being forced under pressure into the lungs. Here it comes into close contact with the blood in the capillaries of the lungs, and imparts to this fluid oxygen in return for waste carbon dioxide. At expiration the hyoid apparatus is lowered and the mouth and nostrils opened, so that air from the lungs escapes to the exterior. This is the only mechanism possible for the frog, for, unlike mammals, the lungs are not contained in a closed cavity, or thorax, but lie in a body-cavity common to the whole of the viscera except the heart.

Nervous System. In order that the frog may function as one whole organism and not as a number of separate parts, and so that it can respond to environmental conditions, it is essential that a collection of organs be developed to convey messages (stimuli) about the body, and thus to effect integration. This is the function of the nervous system. The nervous system may be divided into two parts, (i) the central nervous system, and (ii) the peripheral nervous system. The central nervous system itself consists of (*a*) brain, and (*b*) spinal cord, whilst the peripheral nervous system is made up of (*a*) ten pairs of cranial nerves communicating with the brain, and (*b*) ten pairs of spinal nerves in connexion with the spinal cord. Thus the classification may be summarised—

(i) Central nervous system.
    (*a*) Brain.
    (*b*) Spinal cord.
(ii) Peripheral nervous system.
    (*a*) Ten pairs of cranial nerves.
    (*b*) Ten pairs of spinal nerves.

Each of these parts will be dealt with individually.

(A) Brain. Like that of the other Chordata the brain of the frog is primarily divisible into three regions. These are the fore-brain, mid-brain and hind-brain. The fore- and hind-brains are themselves each further subdivided into two parts, so that in all the brain consists of five regions. These, from in front backwards, are known as the **telencephalon, diencephalon, mesencephalon** (mid-brain), **metencephalon** and **myelencephalon.** At the extreme anterior end of the telencephalon is a pair of small **olfactory lobes,** concerned with the sense of smell. The remainder of the telencephalon consists of a pair of comparatively large, elongated **cerebral hemispheres,** responsible for such phenomena as consciousness, memory and association (see Chapter XXIII). Behind them is a median diencephalon, known also as the **thalamencephalon.** The side walls of this region are thick and are known as the **optic thalami.** From the roof projects the **pineal stalk,** representing the vestigial remains of a third eye of ancestral forms. The floor is produced downwards to form the **infundibulum,** which becomes closely associated with an upgrowth from the roof of the mouth, known as the **hypophysis,** to form the **pituitary body.**

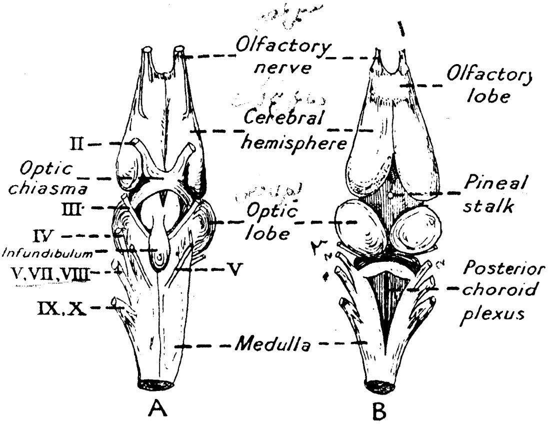


FIG. 101.—*Rana*. Brain. A. Ventral view. B. Dorsal view.

The floor of the mid-brain or mesencephalon is formed of two longitudinal columns of nerve fibres, known as the **crura cerebri,** whereas dorsally this region has become considerably thickened and expanded to form a pair of **optic lobes.** From each optic lobe there passes ventrally an optic nerve. The two nerves run forwards and cross beneath the floor of the posterior end of the telencephalon to form there the **optic chiasma.** Thus each eye is innervated from the optic lobe of the opposite side.

The metencephalon or **cerebellum** is a transverse band of nervous tissue, situated just behind the optic lobes. It functions to co-ordinate muscular movements, as explained in Chapter XXIII. The myelencephalon or **medulla** receives nerves from the greater part of the head, including the ears, as well as a direct supply from the viscera. At its posterior end it passes insensibly into the spinal cord.

The brain itself is hollow, containing in its cavity, as does the spinal cord also, cerebro-spinal fluid. The cavities of the fore- and hind-brain are known respectively as the **third** and **fourth ventricles,** and are connected by the **aqueduct of Sylvius** in the mid-brain. This cavity is itself extended laterally into each optic lobe. The cavity of the fore-brain is further subdivided, for the cavities of the cerebral hemispheres come to be known as the first and second **lateral ventricles,** each communicating with the third ventricle of the diencephalon by a **foramen of Monro.**

The brain is invested in two membranes. The inner one is known as the **pia mater,** and is delicate. It becomes very much infolded into the thin-walled roofs of the diencephalon and the myelencephalon, and is there highly vascularised to form respectively the anterior and posterior **choroid plexus.** Enveloping the pia mater is a tougher, protective **dura mater.**

(B) SPINAL CORD. The spinal cord is an hollow tube contained in the cavity of the vertebral column, including the urostyle. Immediately surrounding the cavity is a collection of nerve cells, constituting the grey matter. This grey matter becomes extended towards the surface in the form of two dorsal and two ventral horns. Enveloping the grey matter, except at these horns, is a cylinder of nerve fibres, constituting the white matter. The significance of this arrangement of nervous tissue will be understood when the paths taken by nervous messages have been discussed in Chapter XXIII. The whole nerve-cord is enclosed in a pia mater, which becomes grooved along the mid-dorsal and mid-ventral lines to form the dorsal and ventral fissures.

(C) CRANIAL NERVES. Issuing from the brain are ten pairs of cranial nerves passing from the cranium through various foramina to supply organs of the head and, in the case of the last two pairs, to run to the viscera. The first pair (No. I) are the **olfactory** nerves. These are not really nerves in the true sense, for they are formed from cells lining the nasal cavity, processes from these cells having become extended backwards to penetrate the olfactory lobes. Similarly, the second cranial nerves, the **optic** nerves, are merely extensions outwards of the brain itself and are not true nerves. Nerve No. III on each side is known as the **occulo-motor,** and together with Nos. IV and VI innervates the eye muscles

The disposition of these latter is precisely the same as that of the corresponding structures in the dogfish, described on page 123. Each occulo-motor nerve supplies all the eye muscles of its own side except the external rectus and the superior oblique. These are supplied respectively by nerves VI (**abducens**) and IV (**trochlear**). Nerve No. V is large and is known as the **trigeminal,** on account of its subsequent division into three branches. Just before it emerges from the skull it bears a swelling, known as a **Gasserian ganglion.** Immediately beyond this it divides into two branches, a **deep ophthalmic** to the skin of the fore-part of the head, and a second branch which, running posteriorly across the orbit, divides into a **mandibular** branch to the lower jaw and a **maxillary** to the upper. The seventh cranial nerve is the **facial,** arising laterally from the myelencephalon just behind the fifth. It penetrates the Gasserian ganglion, with which its own **geniculate ganglion** becomes coalesced, though the two are separate in the tadpole. On emerging from this ganglion it divides into a **palatine** branch to the roof of the mouth, and a **hyomandibular** branch. This latter becomes further subdivided into a **hyoid** branch to the hyoid apparatus and a **mandibular** branch to the lower jaw. Nerve No. VIII is the **auditory,** and is to be regarded as a specialised branch of the facial, with which it therefore arises. It runs into the auditory capsule of its own side to supply the functional part of the ear. The ninth cranial nerve is the **glosso-pharyngeal** and quickly joins the tenth, passing through the ganglion of the latter. It then separates from it almost immediately to become expanded into a **petrosal ganglion** of its own, after which it runs forwards to supply the floor of the mouth and associated structures. The tenth or **vagus** is the largest of them all, and arises by several roots from the posterior end of the myelencephalon. It bears a large **vagus ganglion,** and is concerned with the innervation of the viscera, supplying branches to the larynx, lungs, heart and stomach. On page 124 will be found a table indicating the disposition of the cranial nerves of the dogfish, from which that of the frog differs but little except in respect of nerve VII and the supply to the gill-slits of *Scyllium.*

(D) SPINAL NERVES. There are ten pairs of spinal nerves, emerging on each side through the foramina enclosed between every two successive vertebræ. The last pair arises from two such apertures a short distance behind the front end of the urostyle. It will be observed in dissection that the region of emergence of each nerve is marked by the deposition of a soft, white, calcareous concretion. Each spinal nerve arises by two roots arranged one above the other. The upper one is known as the **dorsal root,** and before leaving the vertebral column, which it does in common with the lower **ventral root,** it bears a swelling termed a dorsal root ganglion. Once outside the vertebral column the two roots join, only to divide again almost at once into a **ramus dorsalis** and a **ramus ventralis.** The former is concerned with the reception of stimuli, which it conveys into the grey matter of the spinal cord. It is therefore described as afferent or sensory. The ramus ventralis, on the other hand, carries messages outwards from the grey matter to the muscles of its own segment, and is described as efferent or motor. From the ramus ventralis arises another short branch, known as the **ramus communicans,** which connects each spinal nerve with a sympathetic nerve-cord running along each side of the dorsal aorta and later to be described. The first spinal nerve of the frog is known as the hypoglossal, and arises behind the first vertebra to supply the tongue. What should really be the first—i.e. a nerve arising in front of the first vertebra—is represented only in the embryo and quickly disappears. The second and third spinal nerves join outside the vertebral column to supply the arm as the **brachial nerve.** The fourth, fifth and sixth remain separate, whilst the seventh, eighth, ninth and tenth become fused to form the **sciatic nerve** to the leg. The seventh and tenth are slender nerves, and the eighth and ninth much stouter.

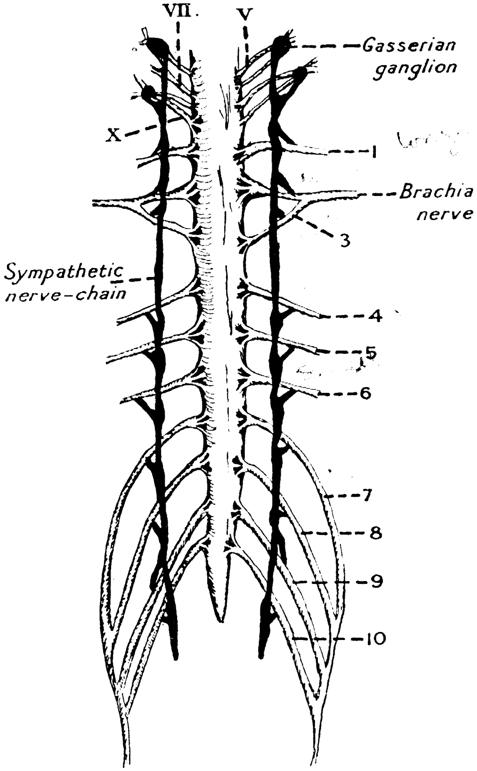


FIG. 102.—*Rana.* Spinal nerves.

(E) SYMPATHETIC NERVOUS SYSTEM. This consists essentially of a slender cord running on each side of the dorsal aorta posteriorly, and diverging in front to accompany each systemic arch. As already pointed out, it is joined by a ramus communicans to each spinal nerve, each junction being marked by a sympathetic ganglion. The cords themselves are double between the first two ganglia, and through each loop thus formed runs a subclavian artery. Anteriorly each sympathetic nerve-cord enters the skull, and establishes a connexion with the tenth nerve before running into the Gasserian ganglion of its own side. The sympathetic nerve-cords are joined at intervals by branches, and are concerned with the innervation of the blood-vessels and viscera. See also page 263.

Sense Organs. There are three paired sense organs in the frog, namely, the nasal organs, the eyes and the ears.

(A) NASAL ORGANS. These are situated one in each nasal capsule, and communicate with the exterior by the nostrils and with the mouth by the internal nares. The lining of each chamber is somewhat folded and is in connexion by the olfactory nerves with the pair of olfactory lobes. Stimulation is brought about by direct contact of particulars of odoriferous substances with the epithelium.

(B) EYES. The eye, as in all the Chordata, consists essentially of a hollow vesicle, the wall of which is three-layered. The outermost layer is the **sclerotic.** This is composed of tough connective tissue and is protective, as well as providing firm ground for the insertion of eye muscles. Anteriorly it is much thinner and becomes transparent, this region being known as the **cornea.** Immediately within this is the **choroid** layer. This is vascularised and is the

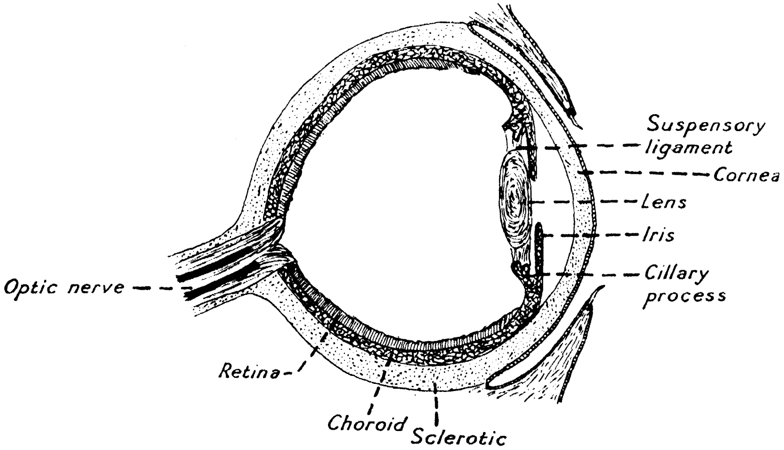


FIG. 103.—Section of vertebrate eye.

nutritive layer of the eye. Anteriorly it is modified, for it becomes separated from the sclerotic layer all round and passes inwards, becoming pigmented to form the **iris.** In the centre of the iris is a large, circular aperture through which the lens is visible. Arising from the choroid coat, just behind the iris, is a pair of projections, one dorsal and one ventral, known as the **ciliary processes,** to which the lens is attached by a pair of **suspensory ligaments.** This body itself is transparent and spherical, and serves to focus light on the sensitive layer at the back of the eye. Together with the iris the lens forms a partition, dividing the cavity of the eye into an anterior and a posterior chamber. The former contains a watery fluid, known as the **aqueous humour,** whereas the posterior chamber is filled with a more viscous **vitreous humour.** The presence of these liquids reduces the amount of refraction of light as it passes into and out of the lens. The base of each ciliary process is connected with the sclerotic coat, where this latter gives rise to the iris, by a ciliary muscle. The innermost layer of the eye is the **retina,** and this is the sensitive layer, being highly pigmented. The optic nerve enters the eye from behind and nerve fibres become spread out over the inner surface of the retina, which they penetrate by turning backwards. The detailed structure of the retina is described on page 266, together with an account of the way in which the eye functions.

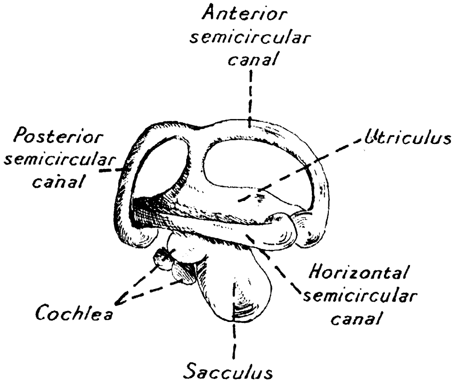

Anterior semicircular canal
Posterior semicircular canal
Utriculus
Horizontal semicircular canal
Cochlea
Sacculus

FIG. 104.—*Rana*. Ear.

(C) Ear. The ear is in principle the same as that of *Scyllium*, but it has no direct communication with the exterior. Each ear lies in an auditory capsule, in which it is supported by a liquid known as **perilymph.** It is essentially an hollow sac, very much evaginated, and contains a fluid known as **endolymph.** It consists of a large **utriculus,** extended ventrally to form a somewhat smaller **sacculus.** From the utriculus there arise three semi-circular canals, an anterior and a posterior vertical at right-angles to each other, and a horizontal canal, all opening into the utriculus at both ends, and each expanded at one end to form an ampulla. In the angle between the sacculus and utriculus lie three short evaginations, representing the **cochlea** of higher forms. The auditory capsule itself is closed off from the cavity of the Eustachian tube by a membrane stretched across the fenestra ovalis, whilst this membrane is connected with the tympanum on the surface of the head by the **columella auris.** Thus vibrations are conveyed first to the tympanum and then through the columella to the membrane over the fenestra ovalis. This sets up vibrations in the perilymph, and these are in turn transferred to the endolymph. Consequently impressions are conveyed to the myelencephalon by the auditory nerve. Only the sacculus apparently serves any auditory purpose, the semi-circular canals functioning to maintain equilibrium.

Urino-genital System. The functions of excretion (elimination of liquid waste products) and elaboration and evacuation of genital products are largely accommodated by the same organs, so that the organs concerned are classified into one composite system. Though the actual excretory organs are similar in both sexes, it will be found convenient to describe the two sexes separately, including both reproductive and excretory organs. It must be first observed that when blood passes through the liver its nitrogenous waste matter is mostly converted into urea. When this blood subsequently reaches the kidneys the urea is extracted, ready for elimination. In both sexes the kidneys are a pair of elongated, oval bodies, reddish in colour, lying dorsally in the posterior part of the abdominal cavity.

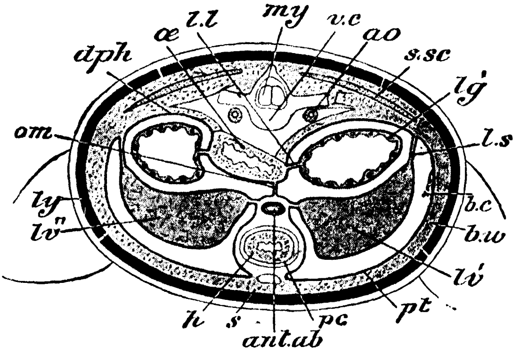


FIG. 105.—*Rana.* Transverse section through trunk in region of œsophagus. (From " Atlas of Practical Elementary Zootomy," by G. B. Howes.)

ao, systemic arch ; *ant.ab*, anterior abdominal vein ; *b.c*, body-cavity ; *b.w*, body-wall ; *dph*, so-called " diaphragm " ; *h*, heart ; *lg'*, right lung ; *l.l*, pulmo-œsophageal mesentery ; *l.s*, suspensory ligament of liver ; *lv'*, the liver, right lobe ; *lv''*, the liver, left lobe ; *ly*, subcutaneous lymph sinus ; *my*, nerve-cord ; *œ*, œsophagus ; *om*, lesser omentum ; *pc*, pericardium ; *pt*, peritoneum ; *s*, sternum ; *s.sc*, suprascapula ; *v.c*, vertebral column.

oviduct becomes expanded to form an egg-sac, ~~where eggs are~~ stored. A bladder occurs, similar in structure and position to that of the male. The oviducts themselves secrete a slimy substance around the eggs, and this expands and hardens to form the characteristic jelly when coming into contact with water.

(C) Reproduction. The breeding season is in March, and pairing occurs. The male climbs on to the back of the female and clasps her with his fore-limbs, maintaining his grip by means of the roughened thumb-pads, which are especially well developed at this season. In this position the frogs may remain for days until the female lays her eggs. When this takes place the male sheds sperms over them, so that there is a reasonably good chance of every egg becoming fertilised. Thus, as in the dogfish, fertilisation is external, but owing to pairing taking place there is reasonable certainty of success.

Ductless Glands. Although these structures are not fully described until Chapter XXIX, it may be useful here to summarise the extent to which they are represented in the frog.

The **thyroid** gland is in the form of a pair of small, rounded structures on the external jugular vein, not far in front of the heart.

The **thymus** is a small, oval gland, lying on either side of the head just within and behind the tympanum.

The **pituitary body,** consisting of **hypophysis** and **infundibulum** (page 152), lies ventral to the floor of the diencephalon.

There is an **adrenal body** situated on the ventral face of either kidney. It is essentially of double origin, consisting of a central **medulla,** of nervous origin, and a peripheral **cortex,** derived from the cœlomic epithelium. In lower forms these two components remain separate as the inter-renal and supra-renal bodies respectively. When these become fused the adrenal bodies are at first not compact, but occur in strips along the sympathetic nerve-cords. This condition is represented in the newt. The pair of carotid glands in the frog, situated at the junction of the internal and external carotid arteries, affords the last remains of these strips.

So far the structure of various systems of the frog has been dealt with. Such a study is known as **morphology.** It is now necessary to pursue this study of structure in greater detail and to investigate the intimate construction of the various organs comprising the systems. This is known as **histology.** Every organ is divided up into a number of units, termed cells. Thus the liver is a collection of liver cells, the brain a collection of nerve cells, and any muscle of the body a collection of muscle cells. A collection of similar cells constitutes a **tissue.** Thus a piece of liver is a tissue.

A very large collection of cells forming a structure which in life exists as one independent whole is an **organ.** Thus the liver, pancreas, heart, spleen, brain and kidney, for example, are all organs, being demarcated quite distinctly from surrounding and associated structures. The following portion of this chapter will be devoted, therefore, to the histology of the various tissues occurring in the frog. This is of especial significance, since the descriptions are applicable to all the Chordate types, tissues being similarly differentiated in all of them.

In order to appreciate the extent to which cellular differentiation has been carried in the frog, it is essential first of all to notice the structure of a typical, unspecialised cell. This cell, as such, does not exist in the frog, the nearest approach to it being the primordial germ-cells, from which the gametes (eggs or spermatozoa) are eventually derived. Such a typical cell is a mass of **protoplasm,** or living matter, bordered by a delicate membrane forming a cell-wall, and containing near the centre a clearly-demarcated region known as the **nucleus.** The substance of which the nucleus is composed is known as **nucleoplasm,** in contradistinction to the **cytoplasm** constituting the remainder of the cell. The description of the detailed structure of the nucleus itself will be reserved until later in this chapter, when the phenomenon of cell-division will be discussed. The cytoplasm itself normally becomes differentiated into a clear, peripheral **ectoplasm** and an inner, granular **endoplasm.** Embedded in this latter, in the vicinity of the nucleus, is a small granule, frequently double, known as the **centrosome,** immediately surrounded by a small area of clear cytoplasm, termed the **centrosphere.** There is also present in the endoplasm rod-like bodies, known as **mitochondria,** and a collection of similarly-shaped structures, forming the **Golgi body.** The cytoplasm itself is variously described as alveolar (foam-like), reticular (of network structure) or granular. Such a simple cell may be imagined as able to effect all its own life-processes, including the absorption and assimilation of food, excretion, respiration and conduction of stimuli, as well as ultimately being capable of division to give rise to two similar cells. But in the frog, consisting of a vast number of cells, specialisation has occurred, so that the cells become adapted to particular functions to the exclusion of others. In this sense they lose their individuality, which thus becomes transferred to the organism as a whole. The various types of tissues encountered in the frog will now be described individually.

Epithelial Tissues. Under this heading are included all those tissues which form a covering to the various surfaces, internal and external. Such a covering may be only one cell thick, in which case the epithelium is described as **simple,** whereas if it is several cells thick the epithelium is said to be **stratified.**

(A) COLUMNAR EPITHELIUM. This consists of somewhat flattened, cylindrical cells placed side by side with little or no space between them, and across such space as does exist the cells are continuous by protoplasmic threads. An example of such a simple epithelium is found in the cells lining the intestine.

(B) CILIATED EPITHELIUM. This closely resembles columnar epithelium, except that the superficial end of each cell bears a number of fine, protoplasmic projections, known as cilia. Ciliated epithelium occurs on the roof of the mouth of the frog. It is a simple epithelium.

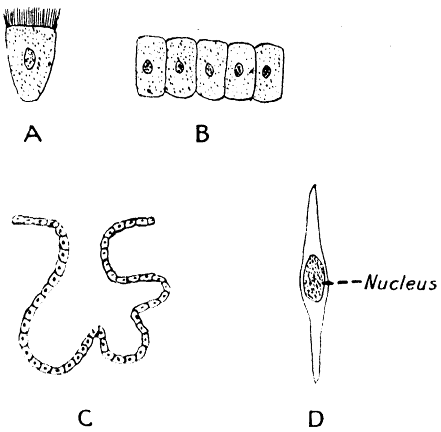


FIG. 108.—*Rana*. Epithelium.
A. Ciliated. B. Columnar. C. Gland.
D. Pavement.

(C) PAVEMENT EPITHELIUM. This consists of flattened cells placed side by side, but separated by spaces occupied by intercellular substance. So thin are the cells that the nuclei may be seen bulging from their surfaces. Such a simple epithelium lines the cœlomic cavity and the blood-vessels.

(D) SENSORY EPITHELIUM. Sensory epithelium is simple and resembles the columnar type. Each cell frequently bears a sensitive process at its superficial end and within is in connexion with a sensory nerve, conveying messages from it to the central nervous system. The epithelium lining the nasal capsules is of this nature.

(E) GLANDULAR EPITHELIUM. Cells comprising glandular epithelium, itself simple, have each become specialised for the elaboration of some specific chemical substance. Such cells may exist in isolation. Thus, lining the intestine there is a large number of cells concerned with the production of mucus. When these have discharged their content they remain hollow for some time until more mucus has been produced : in this condition they are known as goblet cells. A collection of gland-cells constitutes a gland. This may be simple, two or three tubes communicating with the surface by means of a common duct. On the other hand a gland may be racemose. In this case the gland is very much more subdivided, the branches even joining to form a network. The liver and pancreas afford examples of such glands.

(F) SKIN. The most obvious example of stratified epithelium is the skin, covering the entire surface of the body. This is divisible into two layers, the **epidermis** above and the **dermis** beneath. The epidermis itself consists of an outer **Keratin layer** and an inner **Malpighian layer.** The latter consists of actively-dividing cells, their products being pushed towards the surface, where they become worn down to form the Keratin layer. The dermis beneath is a mesodermal layer, composed mostly of connective tissue and containing mucous glands and blood-vessels. The pigment cells occur between the dermis and the epidermis (see Fig. 89).

A reference to germinal epithelium will be made when the maturation of gametes is described.

Skeletal Tissues. These are the tissues concerned with the support of the body or of its individual organs. The blood is included, since it does to some extent serve for support, especially when under pressure. Unlike epithelium there is a great development of inter-cellular substance in skeletal tissues.

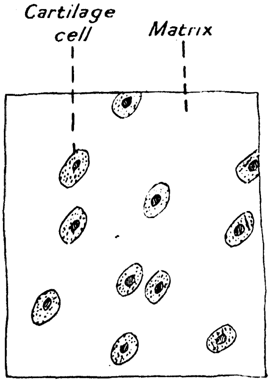


FIG. 109.—*Rana.* Cartilage.

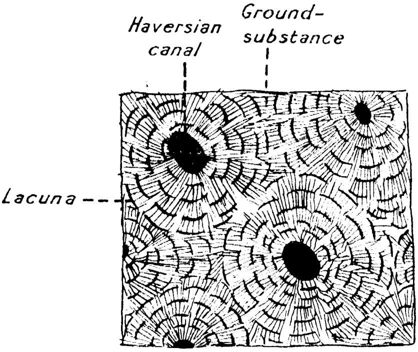


FIG. 110.—*Rana.* Bone.

(A) CARTILAGE. This tissue consists of a groundwork, or **matrix,** in which cartilage cells are embedded. The matrix may contain fibres or remain clear, the cartilage being consequently described as fibrous or hyaline. Calcified cartilage is formed by the impregnation of the matrix with salts of lime.

(B) BONE. This differs from cartilage in that the matrix always contains salts of lime, principally calcium phosphate, and the bone cells are arranged in a regular pattern. The ground substance is arranged in cylinders, or **lamellæ,** separated from each other by spaces known as **lacunæ**, in which the actual living material occurs. In many bones, especially those of the limbs, there is a large, central marrow cavity around which the lamellæ are set. There are also smaller marrow cavities, known as **Haversian canals,** around which are further lamellæ. The lacunæ are connected with each other by **canaliculæ,** running in the ground substance.

(C) CONNECTIVE TISSUE. The ground substance of connective tissue is always fibrous. The fibres are of two kinds, white and yellow. The white fibres each consist of fibrils, they branch but do not join, and have a wavy course. The yellow fibres are straight and branch to form a network: they are not composed of fibrils. In this ground substance lie at intervals spaces containing connective-tissue corpuscles, usually considerably branched. It will be remembered that the dermis consists principally of connective tissue, and the organs of the body are held in position by an investment of this tissue. The limb joints are often strengthened by the presence of tendons. A tendon consists principally of white fibres running parallel to each other.

(D) BLOOD. The ground substance of blood is a liquid, known as **plasma.** In it float the blood cells, or corpuscles, which are of two sorts. There are the red corpuscles, or **erythrocytes,** and the white corpuscles, or **leucocytes.** Each erythrocyte is a small, biconvex disc containing a nucleus. The red blood-corpuscles of mammals are biconcave and enucleate. Each such cell is yellowish in colour, owing to the presence of hæmoglobin. Leucocytes are less in number than the erythrocytes, and both they and their nuclei are of irregular shape. They are capable of amœboid movements and do not contain hæmoglobin. Unlike other cells to which reference has been and will be made, the leucocytes are capable of reproduction by fission.

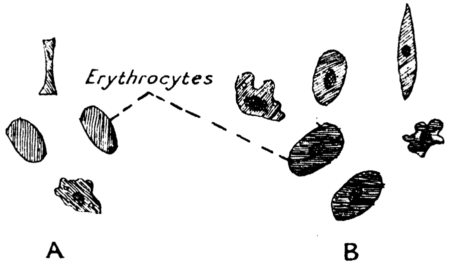


FIG. 111.—Blood corpuscles.
A. Of mammal. B. Of frog.

Muscular Tissues. The cells comprising muscular tissues have become specialised in their immense powers of contraction, this involving only a change of shape and not of volume. There are three types, known respectively as **striped, unstriped** and **cardiac.** A striped muscle consists of fibres large enough to be visible to the naked eye. Each is a **cœnocyte,** that is it is a multi-nucleate mass of protoplasm. The whole fibre is spindle-shaped, and is invested in a thin membrane, known as the **sarcolemma.** There may be seen faint, longitudinal striations passing from end to end, and alternate light and dark bands occur transversely. The nuclei are scattered throughout the entire fibre. Cardiac muscle may be regarded as a modified form of striped muscle. The fibres are rather more blunted in shape and are branched, the branches forming a network, though not actually joining with each other. Each fibre contains but a single nucleus. Unstriped muscle consists of spindle-shaped, uni-nucleate fibres, which frequently branch to form a network. Each fibre is invested in a thin membrane. The striped muscles are described as voluntary, since they can be contracted at will, and are exemplified by the muscles of the limbs. The unstriped muscles are involuntary, since they contract without reference to the will, as with the muscles of the wall of the gut and blood-vessels. The cardiac muscles are confined to the tissues of the heart.

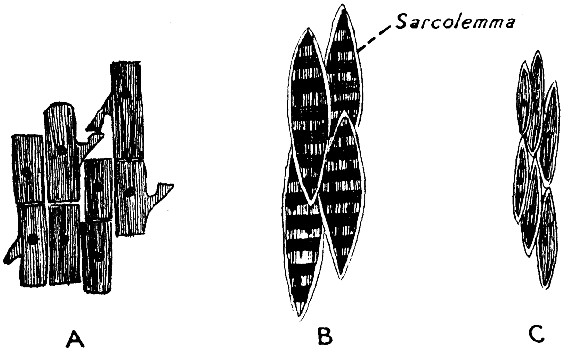


FIG. 112.—*Rana*. Muscular tissues. A. Cardiac. B. Striped. C. Unstriped.

Nervous Tissue. Nerve cells are specialised for the conduction of stimuli from one part of the body to another. It is therefore to their advantage in this respect to have one or more very much elongated processes emanating from the mass of the cell so as to avoid the transference of stimuli from one cell to another. Accordingly, a nerve cell is found to consist of a very much branched cell-body, containing a single nucleus, whilst the branches are known as **dendrites.** The very much elongated process emanating from the cell-body is known as an **axon,** which becomes considerably divided at its free end to form the **terminal arborisation.** Covering the axon or nerve fibre is a delicate membrane, known as the **neurilemma,** beneath which occurs a number of nuclei, presumably associated with it. Nerve fibres are of two sorts, medullated and non-medullated. In the former the axon itself is separated from the neurilemma by a layer of fatty material, known as the **medullary sheath.** This is constricted at intervals to form the **nodes of Ranvier.** In the non-medullated fibres this medullary sheath is absent. The medullated fibres occur in the brain, spinal cord, and cranial and spinal nerves, whilst the non-medullated variety is confined to the sympathetic nervous system. In Chapter XXIX the disposition of cell-bodies and axons in the spinal cord and associated nerves will be discussed.

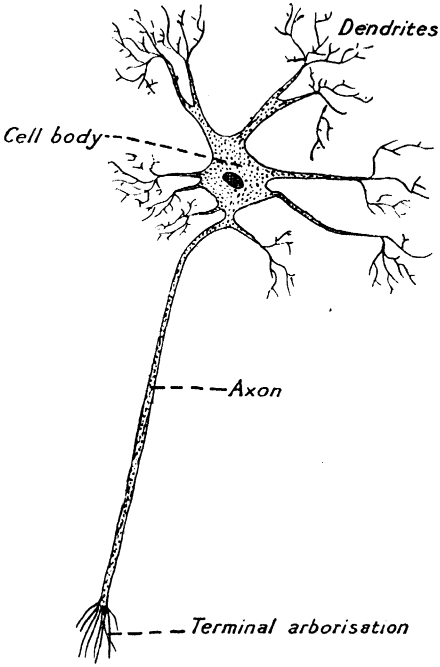


FIG. 113.—*Rana.* Nerve cell.

All the various types of cell described above have been derived by division and differentiation from a fertilised egg. It is now necessary, therefore, to inquire into the process of cell-division, since this forms the basis of all growth. For this purpose a typical cell must first be described. This has to some extent been done already (page 162), but a detailed description of the nucleus must now be given. The nucleus is bordered by a delicate **nuclear membrane,** and within is a network of comparatively dense material, known as **linin,** the interstices being filled with a less opaque **nuclear sap.** Distributed over the linin reticulum are lumps of a readily-stained material, known as **chromatin.** There is frequently found an especially large aggregation of dense material, known as the **nucleolus.** Some authorities hold this to be of cytoplasmic nature. Cell-division involves two distinct processes, namely, the division of the nucleus into two halves, followed by the fission of the cytoplasm. It is believed that this is effected on rare occasions first by the mere elongation of the nucleus, which subsequently becomes

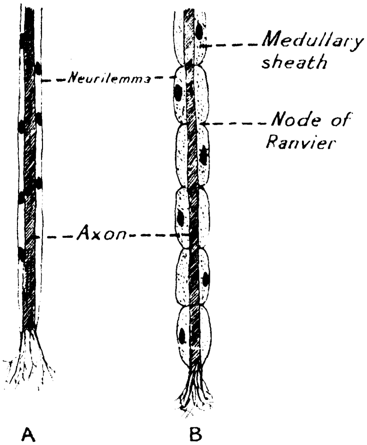


FIG. 114.—*Rana*. Nerve fibres.
A. Non-medullated. B. Medullated.

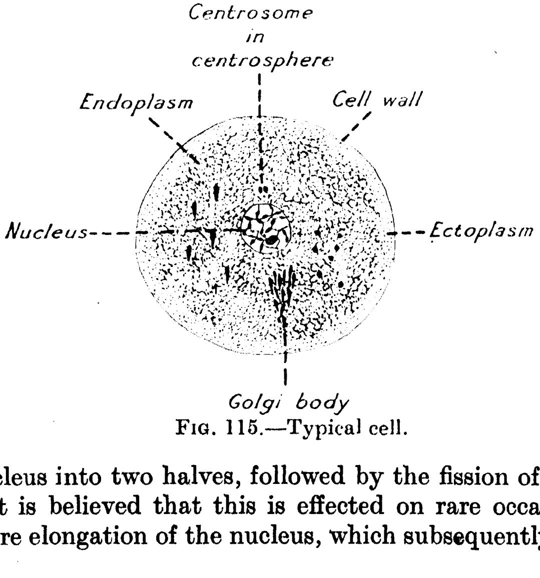
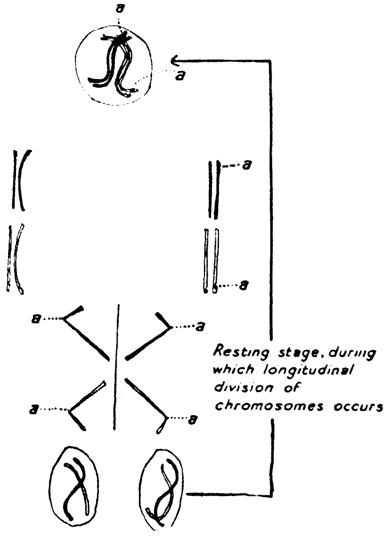


FIG. 115.—Typical cell.

dumb-bell shaped and splits into two halves, followed by the constriction of the cytoplasm along the same line, so that each portion of cytoplasm now contains a daughter nucleus. This simple process of division is known as **amitosis.**

The customary type of division is very much more complicated, and is known as **mitosis.** For purposes of description this is divided up into a number of phases.



Resting stage, during which longitudinal division of chromosomes occurs

FIG. 116.—Mitosis.
a = attachment constriction.

(*a*) *Prophase.* At the outset of mitosis coiled threads appear. These are known as **chromosomes.** It was formerly held that these had not existed as threads before the commencement of the division, but now it is believed that they merely become visible at this stage owing to the precipitation of chromatin granules upon them. These chromosomes are essentially paired structures, for it is possible to find every chromosome, identifiable by its size and shape, duplicated somewhere in the nucleus. In the frog there are twelve pairs of chromosomes. The two members of a pair are described as **homologous,** whilst the number of pairs is described as the **haploid** number (12 in the frog) and the number of single chromosomes as the **diploid** (24 in the frog). In the accompanying figure of mitosis only two chromosomes are considered, for purposes of clarity, since every chromosome behaves in a similar manner. At this stage each chromosome is distinctly longitudinally double, the component halves being termed **chromatids,** which now begin to contract longitudinally to as little as one-twentieth of their original length. It was formerly held that the chromosomes now coalesced to form a long thread, known as the spireme, but this effect is now regarded as an artefact of cytological method. The chromosomes are known to be the carriers of heredity factors, and to have constant properties. It would seem unlikely, therefore, that at every cell-division they should coalesce, only to become separated again almost at once. Still less likely is it that in the resting cell the chromosomes actually disintegrate, for this would necessitate not only their reunion to form the same chromosomes as previously, but also the reunion of the fragments in precisely the same linear arrangement as that occupied prior to disintegration. Instead, as has been pointed out, it is now maintained that the chromosomes do not disintegrate in the resting stage, but that the chromatin falls away from them to render them invisible until the next mitosis is about to commence. In the prophase the chromosomes appear to be granular, the individual granules being known as **chromomeres**. At this stage the two granules comprising the centrosome now separate, enclosing a spindle-shaped region of cytpolasm between them. The two halves of the centrosome eventually come to lie one on either side of the nucleus, so that this latter structure is now completely enveloped in the **nuclear spindle**, as this region of cytoplasm is called. That the nuclear spindle is of different nature from the rest of the cytoplasm is proved by the fact that it can be dissected out.

(*b*) *Metaphase*. The nuclear membrane now disappears and the chromosomes become arranged around the inside of the wall of the nuclear spindle in such a way that each chromatid is attached to some point in the equator of the spindle, the chromatid being modified at this point to form an attachment constriction.

(*c*) *Anaphase*. The two chromatids forming each chromosome now commence to move apart, being separated last at their ends. This process is assisted by the longitudinal extension and transverse contraction of the spindle.

(*d*) *Telophase*. The two chromatids comprising each chromosome now move to opposite ends (poles) of the spindle, so that there is now at each pole the same number of chromatids as there was of chromosomes in the original nucleus. At this stage the cytoplasm now becomes constricted along a line parallel to the equator of the spindle, which thus becomes divided into two halves transversely. In each portion of the cytoplasm there is now half the number of chromatids present in the parent nucleus. The nucleus now undergoes in the reverse direction the changes which occurred during the prophase. During the resting stage which follows each chromatid becomes split longitudinally into two, resulting in the formation of chromosomes, each half of which is again a chromatid.

The following may serve as a summary of the changes occurring at various stages in mitosis.

(*a*) *Prophase*. Chromosomes appear, each composed longitudinally of two chromatids and transversely of chromomeres ; the nuclear spindle is formed from the centrosome.

(*b*) *Metaphase*. The nuclear membrane disappears and the chromatids become attached around the equator of the spindle.

(*c*) *Anaphase.* Chromatids of each chromosome move to opposite poles of the spindle.

(*d*) *Telophase.* Constriction of the cytoplasm occurs and changes take place at each pole the reverse of those occurring in the prophase.

In this way one cell becomes converted into two and each contains a full complement of chromosome material, namely, the diploid number (24) of chromosomes, or the haploid number (12) of pairs of chromosomes.

The essential feature of fertilisation is that it involves the union of a spermatozoön with an egg. Each of these is a cell, containing a nucleus. In fact, the sperm is very little other than nucleus. The eggs are produced by division from the epithelium covering the ovary, and when ripe each is a large, rounded cell containing a considerable amount of yolk and being pigmented in the half in which lies the nucleus. It is covered by a vitelline membrane. Spermatozoa are produced from cells lining the seminiferous tubules of the testes. Each is composed of a head, consisting almost entirely of nucleus, connected by a short neck with a long, lashing tail, which renders the cell motile. There is no centrosome present in the egg, whilst that of the spermatozoön occurs in the neck. At fertilisation such an egg and sperm fuse together. It is apparent, therefore, that some modification of ordinary chromosomal behaviour must occur, otherwise there would be a doubling of the number of chromosomes at every fertilisation, for the nucleus of the sperm penetrates that of the egg to form the nucleus of the zygote (fertilised egg). In actual fact the number of chromosomes is reduced to half the normal in both egg and sperm—i.e. there is only one member of each pair of homologous chromosomes present, so that the chromosome-content of each gamete is haploid. The following description of nuclear division is drawn from the pollen-mother cells of *Tulipa*, though it is to be assumed that it is essentially the same wherever the maturation of germ-cells is taking place. For convenience the process is again divided into a number of phases, and two distinct divisions are involved in effecting this reduction of chromosome-number.

(I) FIRST DIVISION

(*a*) *Prophase.* This phase covers a number of changes, and is therefore subdivided into four stages.

(i) *Leptotene.* The chromosomes appear as single threads, not arranged in any particular configuration.

(ii) *Zygotene.* Homologous chromosomes now come together, and random contact is made. Thus there is now a number of double threads, each component of which is a chromosome, and not a chromatid, as in mitosis.

(iii) *Pachytene.* Chromosomes contract longitudinally.

(iv) *Diplotene.* A split now occurs in each component of each paired thread, so that the threads are now quadruple. This signifies that each chromosome has now split into its two component chromatids.

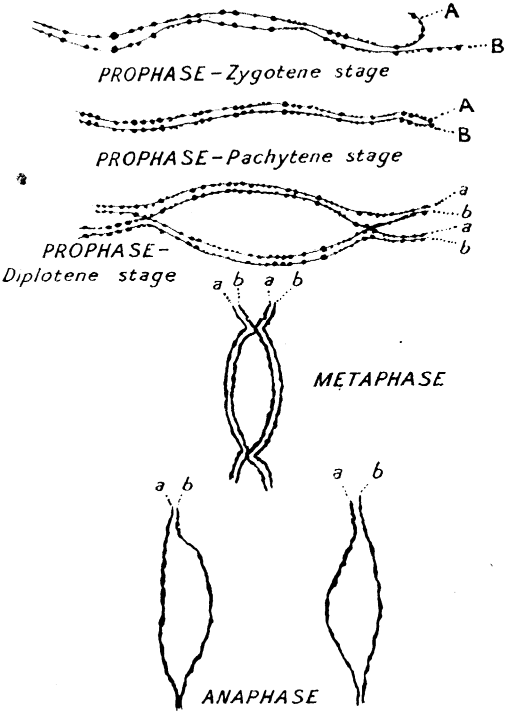


FIG. 117.—First meiotic division.

(*b*) *Metaphase.* A nuclear spindle appears, as in mitosis, and the threads become arranged in its equator. Chromatids from opposite members from each associated pair of chromosomes now become united to each other, and for each united pair of chromatids an attachment constriction is developed, whereby it becomes attached to the spindle in the latter's equator.

(*c*) *Anaphase.* Considering each quadruple thread one pair of united chromatids moves to one pole and the other pair to the opposite pole. Thus every chromosome is represented by a chromatid at each pole.

(*d*) *Telophase.* There is now present the haploid number of chromosomes and diploid number of chromatids at each pole. At this point a resting stage may occur or the nucleus may proceed at once to the second division. In any case cytoplasmic constriction occurs, so that two cells are formed.

(II) SECOND DIVISION

(*a*) *Prophase.* This occurs only if a nuclear wall has been reformed after the first division. Otherwise the nuclei are already in the condition characteristic of the end of the prophase.

(*b*) *Metaphase.* The two chromatids comprising each chromosome move wide apart except at their attachment constrictions. The chromosomes become attached around the equator of the nuclear spindle.

(*c*) *Anaphase.* One chromatid of each chromosome now moves towards one pole and the other chromatid to the opposite.

(*d*) *Telophase.* The chromatids at each pole become surrounded by a nuclear membrane and cytoplasmic constriction occurs. Thus, in all, four cells are formed from a parent cell in these two divisions, and each chromatid now splits longitudinally, the double thread being a chromosome and each component a chromatid. Each cell now contains only the haploid number of chromosomes.

This modified form of nuclear division is known as **meiosis.** It differs from mitosis fundamentally in one respect, and that is that the first meiotic division is commenced prior to the longitudinal splitting of each chromosome into two chromatids.

This typical nuclear division, involving reduction of chromosome-number, is accompanied in Chordata in general by other processes differing in male and female. The maturation of spermatozoa is known as spermatogenesis and that of ova as oögenesis. Each will be described in turn.

(A) SPERMATOGENESIS. Lining the tubercles of the testes are unspecialised cells known as **spermatogonia.** These multiply by ordinary mitosis, and eventually each produces two cells which commence to divide before their chromosomes split longitudinally, and with homologous chromosomes lying side by side. These are the **primary spermatocytes.** Each primary spermatocyte then completes the first meiotic division to form two **secondary spermatocytes,** each of which therefore contains the haploid number of chromosomes. Every secondary spermatocyte then effects the second maturation division to produce two **spermatids,** each of which subsequently undergoes metamorphosis (a series of rapid changes) without further division to form a mature spermatozoön.

This metamorphosis involves the loss of almost all the cytoplasm except for a delicate filament forming the " tail " of the spermatozoön, the head of which is almost naked nucleus.

(B) OÖGENESIS. In the cœlomic epithelium constituting the ovary lie cells known as **oögonia,** corresponding to the spermatogonia of the male. In a comparable manner **primary oöcytes** are formed and then **secondary oöcytes,** containing only the haploid number of chromosomes. At the pachytene stage of the first maturation division a period of rest occurs, wherein reserve food is absorbed. But when a primary oöcyte divides cytoplasmic cleavage is unequal, resulting in the production of a large **secondary oöcyte** and a **first polar body.** The secondary oöcyte now completes the second maturation division and again cytoplasmic cleavage is unequal, one **ovum** and one **second polar body** being formed. The first polar body itself divides to give rise to two further second polar bodies, indicating that it itself is an abortive secondary oöcyte.

The following diagram will serve to summarise the nuclear behaviour in spermatogenesis and oögenesis in the frog, where 12 is the haploid and 24 the diploid number of chromosomes.

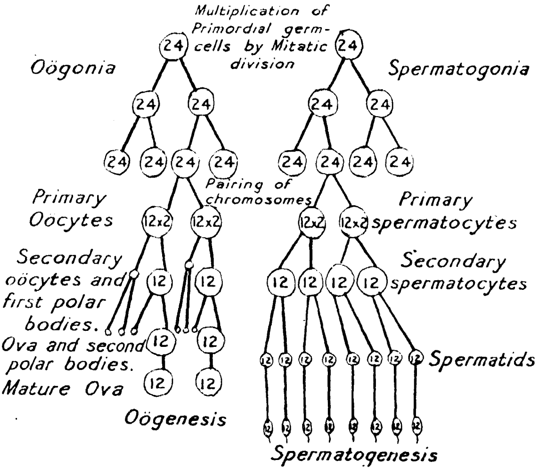


FIG. 118.—*Rana.* Gametogenesis.

CHAPTER XV

LEPUS

THE common rabbit, *Lepus cuniculus*, is well known both in the wild and domesticated condition. It was introduced into Britain by man from the Mediterranean countries, and following its subsequent carriage to Australia it found climatic conditions so suitable in that country that it has become a pest. It lives in burrows, and such are arranged in small communities. It is crepuscular in its habits, this to some extent being a protective adaptation, for the animal is herbivorous and has practically no means of defence against its carnivorous enemies. The rabbit is a member of the class **Mammalia.** Members of this class are characterised by certain diagnostic features. They are warm-blooded, this signifying that the temperature of their blood remains more or less constant. The body is invested in a partial or complete covering of hair, this assisting in the conservation of body-temperature by preventing the loss of heat to the exterior. The young are born alive and are suckled—i.e. they are fed on a milky secretion produced in the mammary glands of the mother.

External Features. The covering of hair to the body of a rabbit is almost complete. At the posterior end the vertebral column becomes extended backwards to form a true tail, invested in skin and fur. The under surface of the tail is white in colour, and this is suggested as being of protective significance to other members of the community, for on approach of danger one individual may the more easily be seen by others to be moving towards its burrow, when the remainder tend to behave similarly. The body is clearly divisible into head, neck, trunk and limbs. Beneath the tail is the anus, through which fæces are shed to the exterior. Ventral to this lies the urino-genital aperture, known in the male as a penis and in the female as a vulva. In the adult male there may be seen on either side of the penis a scrotal sac containing a testis. This is a feature characteristic of the adult males of most mammals. On the head the most conspicuous feature is a pair of long, external ears, or pinnæ, functioning for the collection of sounds. Each eye has an upper and a lower lid, and the transverse eye-lid of the frog is represented in the rabbit by a small nictitating membrane in the inner corner of each eye. The upper lip is deeply cleft in the centre and is known as an hare-lip. On either side of the snout is a number of long, sensitive whiskers, known as vibrissæ. Along the ventral surface of the trunk of the female lie some four pairs of nipples, which contain the apertures of the mammary glands. In both sexes a pair of pits, one on either side of the anus, mark the openings of the **perineal glands,** to whose secretion the characteristic smell of the rabbit is due. The limbs are built on the same plan as in the frog and each digit terminates in a hard claw.

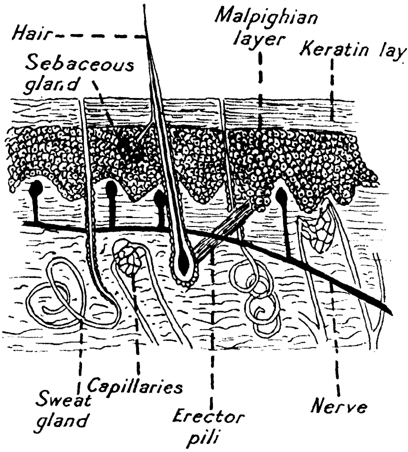


Fig. 119.—*Lepus.* Vertical section of skin.

Skin. The skin is clearly divisible into an ectodermal **epidermis** on the surface and a mesodermal **dermis** within. The former is further subdivided into a superficial **Keratin layer** and an underlying **Malpighian layer.** This latter is composed of actively-dividing cells, the products of this division passing outwards to form the flattened, horny scales of the Keratin layer. The dermis itself is mainly connective tissue, and contains considerable quantities of fat. Running in the dermis are blood-vessels and nerves, the latter acquiring a connexion with sensitive cells of the epidermis. At intervals the innermost layer of the Malpighian layer becomes invaginated to form a pit in the dermis. This is an hair-papilla, cells at the base of which multiply to bring about the growth of the hair. Each hair itself is divisible into a central medulla, surrounded by a pigmented cortex and covered by a thin cuticle. Beneath the dermis occur muscles concerned in the movements of the skin. As well as the structures already described there are three kinds of glands found in the skin, all of epidermal origin. The **sweat glands** are sunk deep into the dermis, where each ends in the form of a much-coiled, blind tube. They are important in the regulation of body-temperature, for they acquire water from neighbouring blood-vessels and this is passed on to the surface. Here evaporation occurs, and the latent heat required to effect this process is obtained from the animal, which thus becomes cooled. **Sebaceous glands** are concerned in the production of the greasy substance associated with the hairs of the rabbit. They are much branched and their secretion is actually elaborated by the cells comprising each gland. The glands open into the hair follicles. The perineal glands belong to this class, as also do the Meibomian glands along the edges of the eye-lids. The secretion of these latter serves to clear the cornea of particles of dust when the rabbit closes and reopens its eyes. The **mammary glands** occur in both sexes but become functional only in the female. Each is a branched tube lying between the dermis and the muscles beneath. They open on to the surface by the nipples. A somewhat remarkable adaptation in the Mammalia in general is the correspondence of the number of nipples to that of young born in a litter.

Skeleton. It is assumed here that the reader will at this point have already studied the skeleton of the frog, so that certain points concerned with general skeleton-construction will now be omitted. The skeleton of the rabbit is almost entirely bony, but it is represented first by cartilage, which subsequently becomes largely replaced by cartilage-bone, whilst membrane-bones contribute a good deal to the skeletal architecture. Each portion of the skeleton will be described in turn, but owing to its greater suitability for practical work the skull of the dog will be substituted for that of the rabbit, though the two are in most respects essentially the same.

(A) VERTEBRAL COLUMN. Like that of the frog the vertebral column is made up of a number of vertebræ articulating end to end to form an hollow tube. Each vertebra consists of a centrum, from which arise two neural arches, joining above to enclose the nerve-cord. In the mid-dorsal line arises a neural spine, whilst transverse processes and articulating surfaces (zygapophyses) also occur. But whereas all the vertebræ of the frog are essentially the same the vertebral column of the rabbit is clearly regionally differentiated, the vertebræ of the various portions being characterised by certain well-defined features.

(i) *Cervical Region.* In all mammals except three species there are seven cervical vertebræ. To each of these there is fused on either side a short cervical rib, the tuberculum of the rib with the transverse process of the vertebra and the capitulum with the centrum. This fusion takes place in such a way as to enclose a foramen through which passes the vertebral artery. This foramen is known in consequence as the **vertebrarterial canal.** The first cervical vertebra is peculiarly modified and is known as the **atlas.** It has no centrum, and in life its cavity is divided transversely by a ligament, the spinal cord passing through the upper chamber and the **odontoid process** of the second cervical vertebra projecting into the lower chamber. The transverse processes are much expanded for the reception of the exoccipital condyles of the skull. The second cervical vertebra, known as the **axis,** is peculiar in that the anterior end of its centrum bears a blunt projection, known as the odontoid process. This is morphologically the centrum of the atlas, having become fused with that of the axis during development.

(ii) *Thoracic Region.* There are usually twelve thoracic vertebræ, characterised by the possession of long, backward-directed neural spines. With each there articulates on either side by means of a double facet a movable rib.

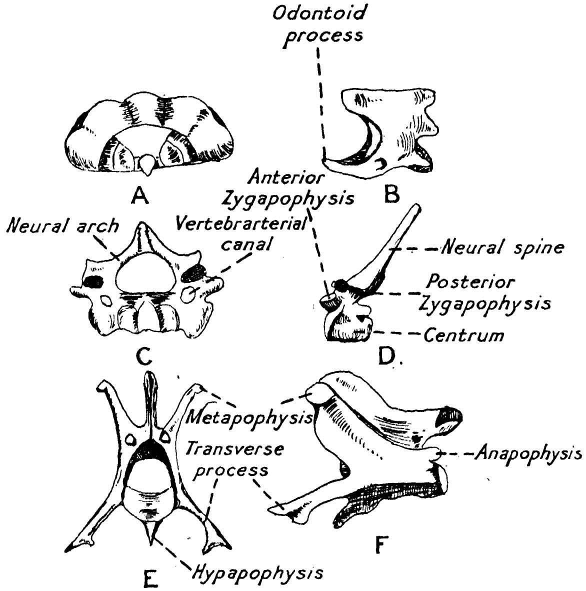


FIG. 120.—*Lepus.* Vertebræ. A. Atlas. B. Axis. C. Cervical. D. Thoracic. E. and F. Lumbar.

(iii) *Lumbar Region.* Seven is the usual number of lumbar vertebræ, which may be distinguished by their large transverse processes. In addition, the zygapophyses are well developed. The anterior zygapophyses are borne each on the inner side of a large **metapophysis,** and the posterior end of the vertebra bears a pair of **anapophyses,** each overhanging the intervertebral notch of its own side.

(iv) *Sacral Region.* This consists usually of one vertebra, but occasionally contains two vertebræ; and receives the ilia of the pelvic girdle, for which purpose expanded processes occur, probably formed by the fusion to the vertebra or vertebræ of sacral ribs.

A number of vertebræ immediately behind this region are fused with the sacral vertebra(e) and the whole mass constitutes the **sacrum.**

(v) *Caudal Region.* This is made up of some eighteen vertebræ. The first two or three are fused with the sacrum, and the hinder ones remain separate, becoming progressively more degenerate till finally they are nothing more than minute rings of bone.

(B) RIBS AND STERNUM. There are twelve pairs of ribs forming the skeletal support for the wall of the thorax or chest. These ribs articulate dorsally with the thoracic vertebræ by a double facet, a **tuberculum** articulating with the transverse process of its vertebra and a **capitulum** with the centrum. The last three pairs of ribs have no tubercula. In the midventral line is the breast-bone or **sternum.** This is divided transversely into six **sternebræ,** the most anterior of which is attached to the clavicle, and to the posterior sternebra is attached a **xiphisternum,** bearing at its free end a plate of cartilage, known as the **xiphoid cartilage.** The first seven ribs on each side articulate ventrally with the sternum, whilst the eighth and ninth are attached to the seventh. The last three end freely at their ventral extremities, and are known as floating ribs.

(C) PECTORAL GIRDLE AND FORE-LIMB. The pectoral girdle is somewhat degenerate when compared with that of lower forms. This may be accounted for by the development of ribs which render it no longer necessary for this girdle to be in the form of a hoop of bone to support this region of the body. The two halves have become completely independent, and each is composed almost entirely of one bone, the **scapula** or shoulder-blade. This bears a ridge, known as the **acromion,** along its outer edge, and a small **coracoid** process, representing the coracoid of lower forms. Joining the acromion to the first sternebra is a slender **clavicle** or collar-bone, whilst along the dorsal border of the scapula runs a narrow rod of cartilage, the **suprascapula.**

The bone of the upper arm, known as the **humerus,** fits into the **glenoid cavity** of the pectoral girdle of its own side. In front of the head of this bone lies the **bicipital groove,** bordered on the inside by the **lesser tuberosity,** which fits into the glenoid cavity, and on the outside by the **greater tuberosity.** Running along the ventral side is a **deltoid ridge.** At the distal end is a groove, known as the **trochlea,** for the reception of the ulna. Just above this, on the front of the bone, is a depression known as the **coronoid fossa,** whilst in a corresponding position on the under surface is an **olecranon fossa** for the reception of a projection of the ulna when the arm is straightened out. The two fossæ are in communication by a **supratrochlear foramen,** pierced in the part of this bone which has become thin owing to the formation of these fossæ. The fore-arm is made up of two separate bones, the **radius** and the **ulna.** In the rabbit these are fixed, but in man the lower end of the radius may be rotated to a limited extent about the ulna. Thus the two bones may lie parallel to each other, as when the arm is stretched forwards with the palm pointing upwards. This position is known as that of **supination.** When the palm is turned downwards rotation of the radius about the ulna occurs and the position is described as that of **pronation.** In *Lepus* the bones are permanently fixed in the prone position. The wrist is composed of three proximal carpals, known as the **radiale, intermedium** and **ulnare,** whilst articulating with these are a central carpal and four distal ones, termed respectively the **trapezium, trapezoid, magnum** and **unciform.** There are five metacarpals, all bearing three phalanges, except the first, which has only two.

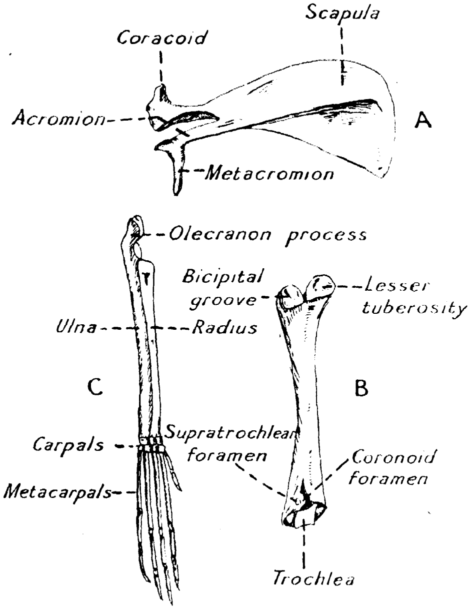


FIG. 121.—*Lepus.* Pectoral girdle and fore-limb.
A. Scapula. B. Humerus. C. Lower limb.

(D) PELVIC GIRDLE AND HIND-LIMB. As in the frog the pelvic girdle consists of two identical halves, fused in the middle line, and each consisting of **ilium, ischium** and **pubis.** The two halves together form a hoop-like structure in the posterior part of the body-wall. Each ilium extends forwards and upwards to become attached to the sacrum. The ilium is continued backwards behind the **acetabulum**—the depression into which fits the head of the femur—as the ischium, whilst ventral and anterior to this lies the pubis.

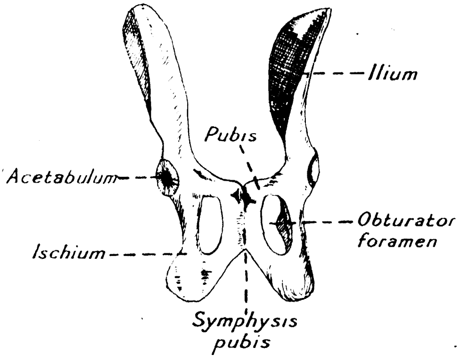


FIG. 122.—*Lepus*. Pelvic girdle.

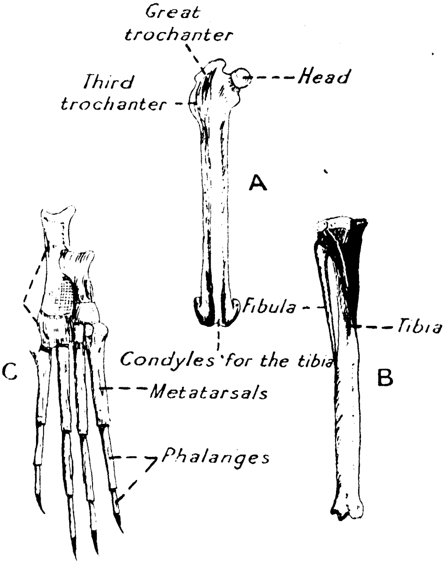


FIG. 123.—*Lepus*. Hind-limb.
A. Femur. B. Tibiofibula. C. Foot.

The ischium and pubis unite to enclose an **obturator foramen,** whilst the two pubes unite in the midventral line to form a pubic symphysis.

The sacrum and two halves of the pelvic girdle together constitute the pelvis. Through the ring of bone thus formed pass both the gut and the urino-genital tract, so that in the female the embryo must also be passed through this ring prior to birth.

The bone of the thigh is the **femur,** the head of which fits into the acetabulum, being expanded for this purpose to form a **lesser trochanter.** On the outer side of the head of the femur lies a **greater trochanter** for the attachment of muscles, whilst below this occurs a **third trochanter.** At the lower end of this bone are two condyles for the reception of the tibia. The shin or lower leg region is formed of a large **tibia** and a slender **fibula,** the two being fused together at their distal ends. The joint between the femur and the tibia is covered by a small bone, known as the **patella** or knee-cap. Along the anterior surface of the tibia runs a prominent **cnemial** crest. The foot consists of two proximal tarsals, known as the **astragalus** and the **calcaneum,** whilst there is one central tarsal and three distal ones. These latter are in reality the second (known as the **mesocuneiform**), the third (the **ectocuneiform**) and the fused fourth and fifth (the **cuboid**). There are only four metatarsals, each bearing three phalanges.

(E) SKULL. In the following description the skull of the dog will be taken as typical of that of mammals. A knowledge of the skull of the frog will be assumed. Considering first the cranium, the floor consists, from the back end forwards, of the **basioccipital, basisphenoid, presphenoid** and **vomer.** This is not homologous with the vomer of the frog, but represents the anterior end of the parasphenoid of the latter type. The roof consists of a **supraoccipital** (above the foramen magnum), and paired **parietals, frontals** and

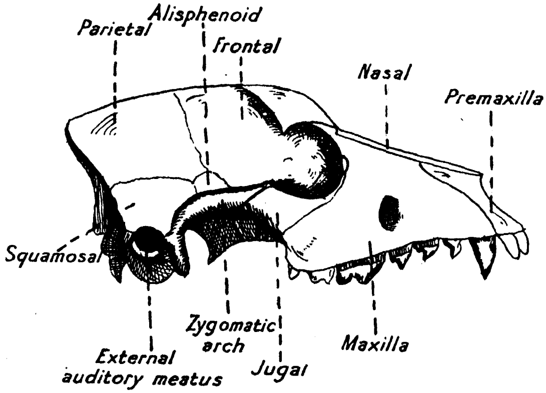


FIG. 124.—Skull of dog. Lateral view.

nasals. The side wall of the cranium is made up of **squamosal, alisphenoid** and **orbitosphenoid** on each side, whilst near the front end of the orbit occurs a small **lachrymal** bone. The **sphenethmoid** has become modified to form a **cribriform plate,** placed transversely so as to limit the forward extension of the cranial cavity. It is continued in front of this as a median, vertical plate of cartilage separating the right and left nasal chambers. The cribriform plate itself is pierced by holes through which pass branches of the olfactory nerves. Within the nasal cavities is a number of very thin **turbinal** bones supporting the nasal epithelium. The auditory capsules are each bordered by a number of bones, which have become fused to form the **periotic.** The tympanic cavity leading from the ear is enclosed in a flask-shaped membrane-bone, the **tympanic bulla.**

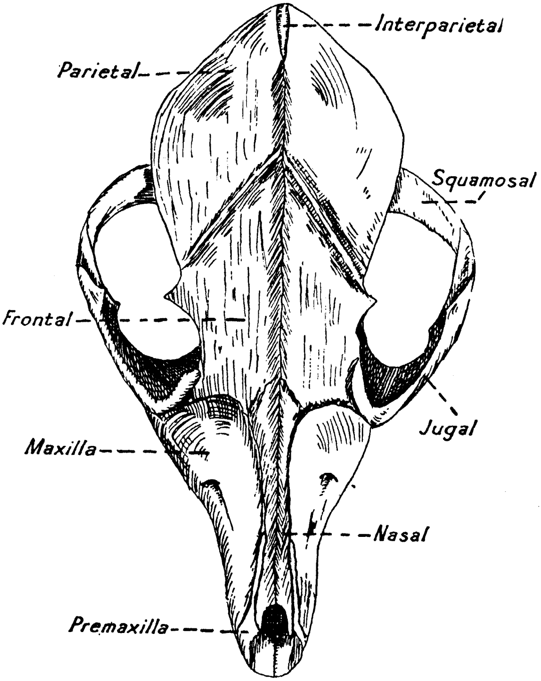


FIG. 125.—Skull of dog. Dorsal view.

Since the brain is thus enclosed within a bony cranium it is essential that foramina be pierced to permit the passage to and from the brain of nerves and blood-vessels. As the bones constituting the skull enlarge during development they meet each other, forming sutures. In many cases a foramen is formed by two bones failing to meet over a small area, but in other cases a bone may grow round a nerve or blood-vessel, present before the development of the bone, to form a foramen actually piercing the bone in question. Most of the important foramina occur in the orbit and posterior end of the skull. Starting posteriorly and working forwards, nerve XII passes through a **condylar foramen** in the exoccipital.

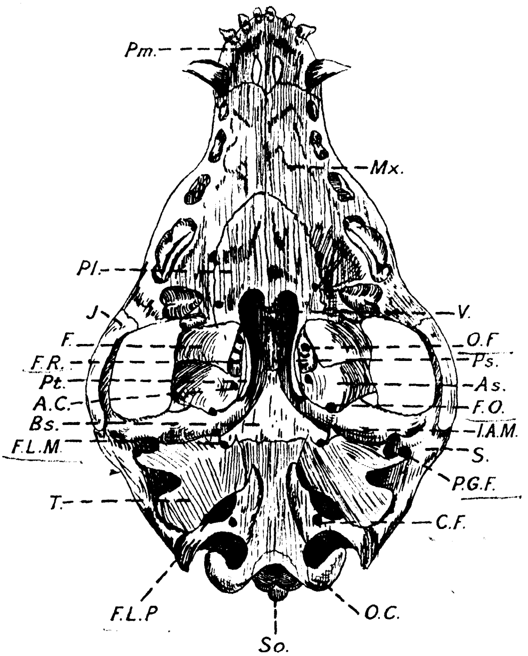


Fig. 126.—Skull of dog. Ventral view.

A.C., alisphenoid canal; *As.*, alisphenoid; *Bs.*, basisphenoid; *C.F.*, condylar foramen; *F.*, frontal; *F.L.M.*, foramen lacerum medium; *F.L.P.*, foramen lacerum posterius; *F.R.*, foramen rotundum; *F.O.*, foramen ovale; *I.A.M.*, internal auditory meatus; *J.*, jugal; *Mx.*, maxilla; *O.C.*, occipital condyle; *O.F.*, optic foramen; *P.G.F.*, post-glenoid foramen; *Pl.*, palatine; *Pm.*, premaxilla; *Ps.*, presphenoid; *Pt.*, pterygoid; *S.*, squamosal; *So.*, supra-occipital; *T.*, tympanic; *V.*, vomer.

Just in front of the exoccipital, between it and the periotic, is the **foramen lacerum posterius,** through which pass nerves IX, X and XI, together with the internal jugular vein. Between the tympanic bulla and the periotic is the **stylomastoid foramen** for nerve VII. The outer opening of the tympanic bulla is known as the **external auditory meatus.** The **Eustachian canal,** leading into the tympanic bulla, passes between the latter and the basisphenoid. Just median to this is the **foramen lacerum medium** for the entry of the internal carotid artery. There is a canal in the alisphenoid, but it is not a true foramen since it does not enter the skull. The external carotid artery which passes through it penetrates the alisphenoid, in which it runs for some distance before emerging again still on the outside of the skull. The mandibular branch of nerve V emerges through the **foramen ovale,** situated between the periotic and the alisphenoid. In the alisphenoid itself is a **foramen rotundum,** through which passes the maxillary branch of V. Between the alisphenoid and the orbitosphenoid lies the **foramen lacerum anterius,** through which pass nerves III, IV and VI, and the ophthalmic branch of V. In the orbitosphenoid bone itself is the **optic foramen** for nerve II.

The upper jaw is formed by a pair of **premaxillæ** and **maxillæ.** From the hind end of each of the latter is a backward-projecting **jugal,** which meets a process of the squamosal to form the **zygomatic arch.** The floor of the cranium is partly shut off from the cavity of the mouth by a **false palate.** This is formed by inward extension of the maxillæ and by the **palatines,** continuous behind with them. Each meets the corresponding bone from the other side in the middle line. In this way a separate nasal passage is cut off from the general cavity of the mouth. Just behind each palatine is a small **pterygoid.**

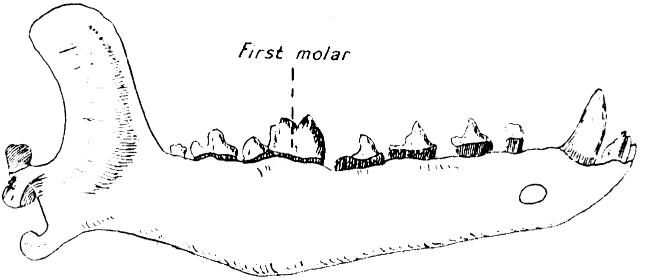


FIG. 127.—Skull of dog. Lower jaw.

The lower jaw consists of only one bone, known as the **dentary,** articulating with the squamosal. The fate of the articular and quadrate is discussed in Chapter XXIV.

The inner opening of the auditory capsule, the fenestra ovalis, is connected with the tympanum by a chain of three bones, known as the ear-ossicles. They are the **stapes** (next the fenestra ovalis), **incus** and **malleus,** abutting on to the tympanum. The significance of these bones is also discussed in Chapter XXIV.

The only other portion of the visceral skeleton surviving is the **hyoid.** It consists of a median plate of bone and two pairs of

Table I. Bones Comprising the Skull

Region of Skull	Cartilage-bones	Membrane-bones
Floor	Basioccipital Basisphenoid Presphenoid Pterygoid	Vomer
False palate	Maxillæ Palatines	
Roof	Supraoccipital	Parietals Frontals Nasals
Side wall	Periotic Tympanum Alisphenoid Orbitosphenoid	Squamosal Lachrymal
Upper jaw		Premaxilla Maxilla
Lower jaw		Dentary
Zygomatic arch		Jugal Squamosal
Ear ossicles	Stapes Incus Malleus	

Table II. Foramina of the Skull

Foramen	Position	Structure passing through
F. magnum	Posterior end of skull	Spinal cord
Condylar f.	In exoccipital	Nerve XII
F. lacerum posterius	Between periotic and exoccipital	Nerves IX, X, XI and internal jugular vein
Stylomastoid f.	Between tympanic bulla and periotic	Nerve VII
F. lacerum medium	Between tympanic bulla and basisphenoid	Internal carotid artery
Eustachian canal	Between tympanic bulla and basisphenoid	Eustachian tube
F. ovale	Between alisphenoid and periotic	Mandibular branch of nerve V
F. rotundum	In alisphenoid	Maxillary branch of nerve V
F. lacerum anterius	Between alisphenoid and orbitosphenoid	Nerves III, IV, VI and ophthalmic branch of V
Optic f.	In orbitosphenoid	Nerve II

backward-projecting cornua. A pair of small, anterior cornua connect the hyoid with the periotic.

Fundamentally the skull of the rabbit resembles that of the dog, except for the numbers of different types of teeth, as described in the account of the digestive system.

The main characteristics of the skull may be summarised in the tables on page 186, concerned respectively with the bones comprising the skull and the foramina pierced in or between them.

Internal Anatomy. As with the frog the organs of the rabbit are segregated into a number of distinct systems, each of which will be described individually.

Alimentary System. The margin of both jaws is bordered by a single layer of teeth. These, unlike those of the frog, are of different types. Thus the dentition of the rabbit, and of mammals in general, is described as **heterodont,** whereas that of lower Chordates is **homodont,** all the teeth being alike. The front teeth of the mammal are known as the **incisors,** and are sharp-edged for cutting. Those of the upper jaw are four in number in the rabbit, and are set two in each premaxilla. In the lower jaw there are two incisors, one on either side of the middle line. In the rabbit there is a long, toothless space on each side in both jaws immediately behind the incisors. This is known as the **diastema.** In most mammals, and especially in carnivorous forms, this is occupied by a **canine** tooth, one in each space. These are well developed in the dog. Behind the diastema in each jaw of the rabbit lie the double teeth, regionally differentiated into **premolars** in front and **molars** behind. Mammals have characteristically only two generations of teeth, the deciduous teeth of the young being later replaced by a permanent set. This condition is described as **dipyhodont,** in contrast to the **polyphyodont** condition in lower Gnathostomata, where there is continuous replacement of teeth throughout life. The premolar teeth can be distinguished from the molars in mammals only by the fact that the latter are not represented at all in the deciduous set, there being only one generation of these. The numbers of various types of

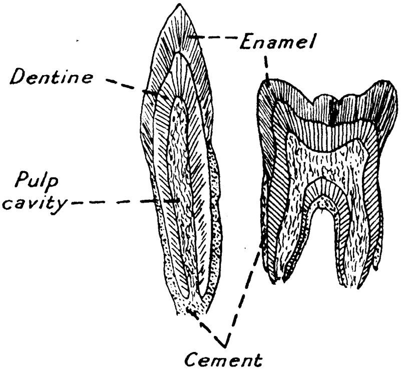


FIG. 128.—Sections of mammalian teeth.

teeth may be clearly and simply represented by means of a **dental formula.** The types are expressed by their initial letter, followed by a fraction, the numerator of which states the number of that kind of tooth on each side in the upper jaw, whilst in the denominator is expressed the same character of the lower jaw. Thus the dental formula of the rabbit is—

$$\mathrm{i}\,\frac{2}{1},\ \mathrm{c}\,\frac{0}{0},\ \mathrm{pm.}\,\frac{3}{2},\ \mathrm{m}\,\frac{3}{3},$$

whilst that of the dog is—

$$\mathrm{i}\,\frac{3}{3},\ \mathrm{c}\,\frac{1}{1},\ \mathrm{pm.}\,\frac{4}{4},\ \mathrm{m}\,\frac{2}{3}.$$

The incisor teeth of the rabbit are peculiar in that they grow perpetually throughout life. They differ from most mammalian teeth in that their pulp-cavities remain open and thus the teeth are continuously supplied with nourishment. They are described as having persistent palps. Those of each jaw are worn down by rubbing against those of the other jaw during the rabbit's characteristic "nibbling" of food. The loss of an incisor tooth may well prove fatal to a rabbit, since the one normally grinding against it would continue to grow unchecked.

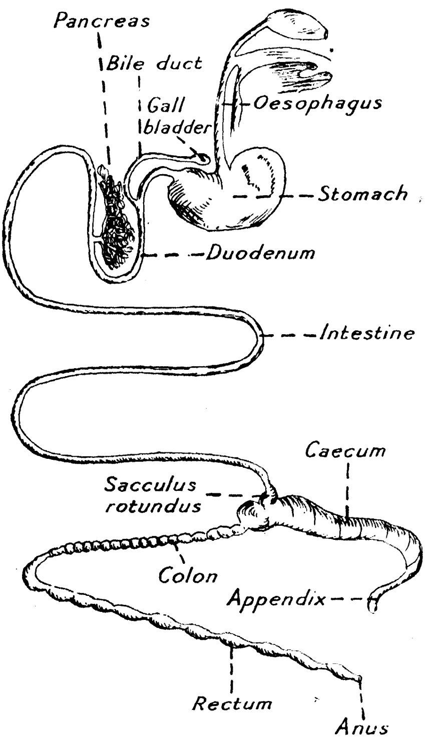


FIG. 129.—*Lepus.* Alimentary canal.

The mouth itself is bordered by a pair of fleshy lips, whilst inside is set the tongue. The false palate of bone already referred to (page 185) is continued by a soft palate of non-bony material, so that the nasal cavities open far back into the dorsal side of the mouth, the opening being known as the secondary choana. From the mouth a narrow tube, the **œsophagus,** leads to the **stomach,** passing on its way through the diaphragm. The stomach itself is a large, sac-like organ lying across the body-cavity just beneath the **diaphragm.** At its distal (pyloric) end it opens into a narrow U-shaped **duodenum,** the opening being closeable by a sphincter muscle. The duodenum leads into a long, spirally-coiled **intestine,** being some seven feet in length and ending in a swelling known as the **sacculus rotundus.** From this there arises a blind diverticulum, known as the **cæcum,** which ends in the form of a narrow **appendix.** The gut itself is continued from the sacculus in the form of a wide, sacculated **colon,** leading into a narrow **rectum,** which communicates with the exterior by the **anus.**

Separate from the gut but communicating with it by ducts are two important digestive glands—the **liver** and the **pancreas.** The liver is a large, red organ, subdivided into five lobes. In the posterior end of the right central lobe lies the **gall-bladder,** communicating by the **bile-duct** with the duodenum not far beyond the pyloric sphincter muscle. The whole liver is attached by a **falciform ligament** to the diaphragm. The pancreas is a pinkish organ situated between the two arms of the duodenum, where it is supported by a fold in the peritoneum. It opens by a pancreatic duct into the distal limb of the duodenum a short distance beyond the bend.

The process of digestion is effected by the treatment of the food with a number of digestive juices. To facilitate this process the food is masticated in the mouth so as to increase its surface-area. In the mouth the food encounters **saliva.** This is produced in four pairs of glands—the submaxillary, the infraorbital, the parotid and the sublingual—and is conveyed to the mouth by ducts. It contains an enzyme known as **ptyalin,** which acts on starch and glycogen, converting them to maltose ($C_{12}H_{22}O_{11}$). The food is then rolled by the tongue into pellets and swallowed, passing along the œsophagus into the stomach. Here it encounters **gastric juice** and **hydrochloric acid,** both produced by gland cells lining the stomach.

The gastric juice contains two enzymes—**pepsin** and **rennin.** The former acts on proteins, converting them into peptides. Rennin curdles milk, converting its soluble caseinogen into insoluble casein. This is important in the young animal, fed on milk by the mother, since the curdling of the milk causes it to be retained longer in the stomach and thus to be more fully acted upon by the pepsin. The hydrochloric reaches a strength up to $\frac{N}{10}$. It is essential for the action of pepsin, as well as which it effects the hydrolysis of maltose and sucrose, according to the equations—

$$\text{(i)}\ \underset{\textit{Sucrose}}{C_{12}H_{22}O_{11}} + H_2O \rightarrow \underset{\textit{Glucose}}{C_6H_{12}O_6} + \underset{\textit{Fructose}}{C_6H_{12}O_6}$$

$$\text{(ii)}\ \underset{\textit{Maltose}}{C_{12}H_{22}O_{11}} + H_2O \rightarrow \underset{\textit{Glucose}}{2C_6H_{12}O_6}$$

The acid also stops salivary digestion and regulates the opening and closure of the sphincter muscle. A certain quantity of lipase (see later) is also present in gastric juice, but owing to the concentration of the acid it is unable to effect any active digestion.

In the duodenum the food meets first the **bile** and then the **pancreatic juice.** The bile itself is usually green in colour, owing to the presence of **biliverdin,** a decomposition product of hæmoglobin. In man it is golden yellow, since it contains **bilirubin.** It contains also the sodium salts of certain organic acids, as well as a small amount of protein material. It serves to emulsify fats, as well as forming soaps from the fatty acids liberated by the pancreatic juice. This process is the same as that described for the frog on page 144.

The **pancreatic juice** contains three enzymes. **Amylase,** like ptyalin, hydrolyses starch and glycogen, converting them to maltose. **Lipase** is responsible for the hydrolysis of fats into fatty

Region	Juice	Enzyme	Substance Acted Upon	End-product
Mouth	Saliva	Ptyalin	Starch and glycogen	Maltose
Stomach	Gastric juice	Pepsin	Proteins	Peptides
		Rennin	Caseinogen	Casein
	Hydrochloric acid		Maltose	Glucose
			Sucrose	Glucose and fructose
Duodenum	Pancreatic juice	Amylase	Starch and glycogen	Maltose
		Lipase	Fats	Glycerine and fatty acids
		Trypsinogen		
		Erepsin	Peptides	Amino-acid
		Maltase	Maltose	Glucose
Intestine	Succus entericus	Enterokinase (Trypsin)	Proteins	Peptides
		Erepsin	Peptides	Amino-acids
		Lactase	Lactose	Glucose and galactose
		Maltase	Maltose	Glucose
		Sucrase	Sucrose	Glucose and fructose

acids and glycerine. As in the frog **trypsin** is secreted as inactive **trypsinogen,** becoming activated later.

The **succus entericus** or intestinal juice contains a number of enzymes. **Erepsin** causes the conversion of peptides to amino-acids, whilst **sucrase** brings about the inversion of sucrose to glucose and fructose. The trypsinogen, of pancreatic origin, meets **enterokinase,** the two together constituting active trypsin, which is responsible for the formation of peptides from proteins. **Maltase** and **lactase** hydrolyse maltose and lactose respectively, the former becoming converted into glucose and the latter into glucose and galactose. Maltase and erepsin are believed to be present also in the pancreatic juice. The table on page 190 may be useful as a summary of the action of the various digestive juices.

In the intestine the food thus liquefied is absorbed. The internal surface of this region is thrown into folds, each of which is a villus. Along the lining of the ventral side of the intestine lie areas of specialised, lymphatic tissue, known as **Peyer's patches** and associated with absorption. Thus liquid food is passed eventually into the blood for distribution.

Respiratory System. The respiratory organs of the rabbit are a pair of lungs, situated in the thorax, this cavity being completely shut off on all sides. From the nostrils a nasal chamber leads backwards and opens into the hind end of the roof of the mouth by the **secondary choana.** Here it crosses the œsophagus in a region known as the pharynx. The **trachea** or windpipe then passes anterior to the œsophagus through the neck. The upper part of this trachea is known as the **larynx.** It is supported by two hoops of cartilage, known as the **thyroid** and **cricoid,** and contains the vocal cords in the form of folds in the mucous membrane. The opening of the larynx into the mouth is protected by a flap of cartilage, known as the **epiglottis.** In swallowing this serves to close the opening of the larynx, and thus prevents the passage of food into the trachea. An Eustachian tube opens into the cavity of the mouth on either side of the nasal passage, whilst just behind these openings are the tonsils, themselves remnants of the second pair of visceral gill-pouches. The anterior end of the trachea is supported by a hoop of cartilage, known as the **arytenoid.** At its base the trachea forks into two **bronchi.** Each of these passes into a lung, where it becomes much more subdivided, first into **bronchioles** and then into tubes of capillary dimensions, termed **alveoli.** The processes of inspiration and expiration are an interesting and important contrast to those in the frog. At inspiration the diaphragm is lowered and the thorax expanded. This causes a reduction in the pressure *on* the lungs, since the thorax is a completely closed chamber. But the pressure *in* the lungs is atmospheric, since they are in open communication with the exterior. Air, therefore, enters the lungs. At expiration the thoracic wall is collapsed and the diaphragm is raised, so that air is now forced out of the lungs by an increase of pressure on their outer surface. A few facts concerning the chemistry of respiration will be found in Chapter XXVI.

Vascular System. This is built on the same plan as that of the frog, but the separation of pure and impure blood is more efficiently carried out, since there are separate right and left ventricles.

(A) HEART. The heart is divided into a right and left auricle and a right and left ventricle. Into the right auricle open the three great veins returning blood from all parts of the body except the lungs. The left auricle receives the conjoined **pulmonary veins** from the lungs. Each auricle is in communication with the ventricle of its own side, but the right and left sides of the heart are completely shut off from each other. The right ventricle is thick-walled but is smaller than the left. From it emerges the **pulmonary artery** to run to the lungs. The left ventricle is large and very thick-walled, and from it arises the **aorta,** along which blood passes for distribution to all the tissues of the body, again excepting those of the lungs. As in the frog the various apertures of the mammalian heart are

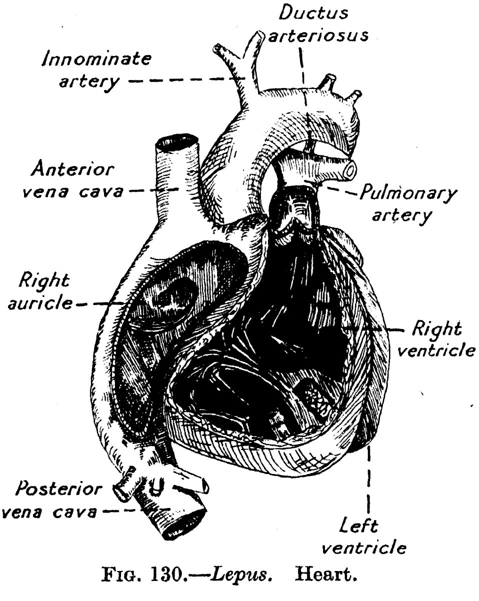


FIG. 130.—*Lepus.* Heart.

guarded by valves. A **tricuspid** valve guards the right auriculo-ventricular aperture, whilst the base of the pulmonary artery is guarded by three **semi-lunar valves.** The **mitral valve** is found at the left auriculo-ventricular aperture, and differs from the tricuspid in that it consists of only two membranous folds. The base of the aorta is set with semi-linar valves.

Thus the general course of blood-circulation in the rabbit may be summarised in Figure 133.

(B) ARTERIAL SYSTEM. The **aorta** leaves the left ventricle, quickly curving to the left and then backwards to run beneath the

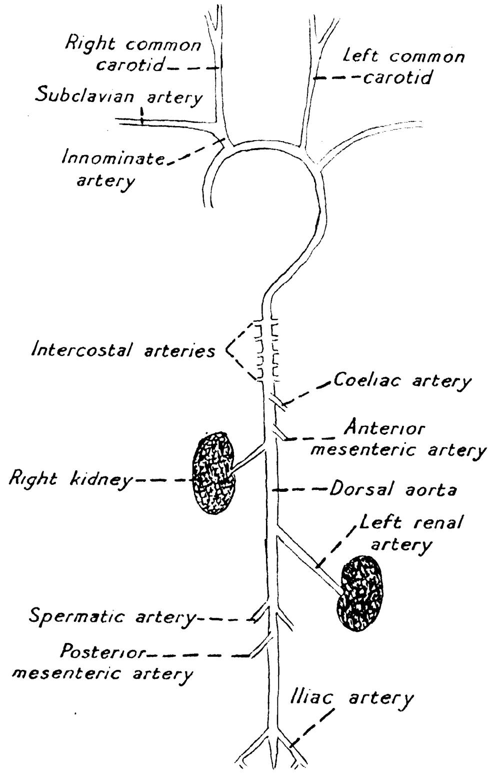


FIG. 131.—*Lepus.* Arterial system.

apex of the heart, from which point onwards it is termed the **dorsal aorta.** Soon after leaving the heart it gives off a short **innominate** artery, which forks to form the **right subclavian** to the arm and the **common carotid** to the head. Further from the heart a **left common carotid** artery arises, and a little behind it a **left subclavian** passes to the arm. The aorta then comes to run in the mid-dorsal line, and during its passage along the back it gives off a **cœliac** artery, which divides to form an **hepatic** to the liver and a **lieno-gastric** to the spleen and stomach. Behind it arises a median **anterior mesenteric,** and laterally, at much the same level, the **right renal** artery is given off. The **left renal,** in accordance with the asymmetric position of mammalian kidneys, arises more posteriorly. Farther back arises a median **posterior mesenteric** artery, as well as a pair of arteries (**spermatic** or **ovarian**) to the genital organs. At its hind end the dorsal aorta gives off an **iliac** artery to either leg, whilst it itself is continued into the tail as the slender **caudal** artery.

A point of evolutionary significance in respect of the blood-system is a ligamentous band, the **ductus arteriosus,** connecting the aorta with the common pulmonary artery.

It has already been pointed out that the red corpuscles of mammalian blood are biconcave and enucleate.

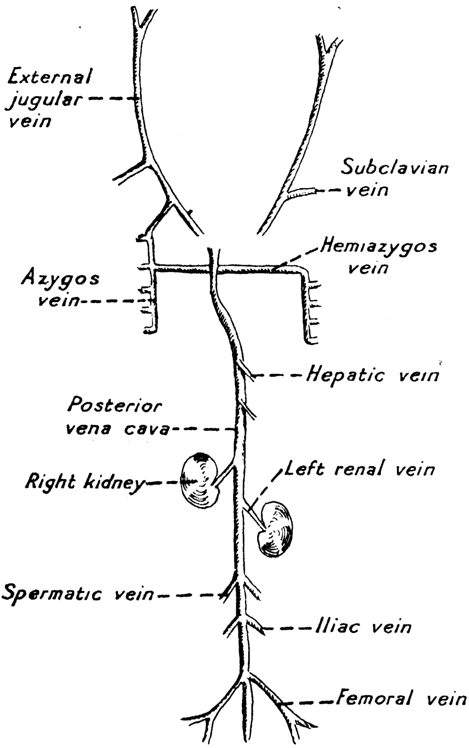


FIG. 132.—*Lepus.* Venous system.

(C) VENOUS SYSTEM. Unlike the frog and dogfish the rabbit has no sinus venosus. Deoxygenated blood is returned from all parts of the body by three great veins, opening independently into the right auricle. Each of the two **anterior venæ cavæ** consists of a conjoined **subclavian** and **jugular** vein, the latter becoming further subdivided into a small internal and large external branch. The right anterior vena cava receives the **azygos** vein from the ribs of its own side and the **hemiazygos** from the corresponding structures of the left-hand side. The **posterior vena cava** receives many branches on its journey to the heart. From each leg comes a

femoral vein, and there arises a pair of **iliacs** from the pelvic region. **Spermatic** or **ovarian** veins return blood from the genital organs, whilst a pair of asymmetrically-placed **renal** veins communicate with the kidneys. Blood from the liver is passed into the posterior vena cava by the **hepatic** veins.

There is no renal portal system in mammals, but blood is conveyed from the stomach and intestine to the liver *viâ* an **hepatic portal** vein, which disintegrates within the tissues of the liver so that carbohydrate food may be extracted and stored as glycogen.

Lymphatic System. Much of the dissolved food finds its way into the lymph-vessels associated with the great veins of the body. The majority of them eventually open into the thoracic duct, communicating with the left subclavian vein near its union with the jugular vein. The lymphatic vessels from the right side of the anterior part of the body open into the right anterior vena cava.

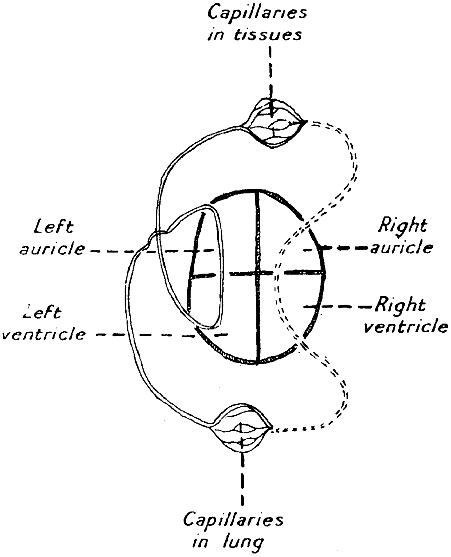


FIG. 133.—Mammalian circulation. Dotted lines show course of de-oxygenated blood.

Nervous System. The general classification of the nervous system into its component parts is the same as that of the frog (page 151). It is principally in respect of the brain that specialisation has occurred, and thus in the mammal this organ shows a very considerable advance on anything previously encountered.

(A) BRAIN. This organ may be subdivided into the same five parts as that of the frog. The telencephalon consists of a pair of very much enlarged **cerebral hemispheres,** extended backwards completely to cover the mid-brain. Each hemisphere is subdivided superficially into a number of lobes by fissures. Laterally at about the middle of its length occurs a **Sylvian fissure,** dividing a **posterior temporal** lobe from the remainder, whilst ventrally a longitudinal **rhinal** fissure separates a **rhinencephalon** towards the middle line from a **frontal** (anterior) and **temporal** (posterior) lobe laterally. The rhinencephalon itself is transversely divided into an anterior **olfactory** lobe and a posterior **hippocampal** lobe. The former is continued forwards to end in a small olfactory bulb. The two cerebral hemispheres are connected by a transverse band of fibres, known as the **corpus callosum,** a development peculiar to mammals.

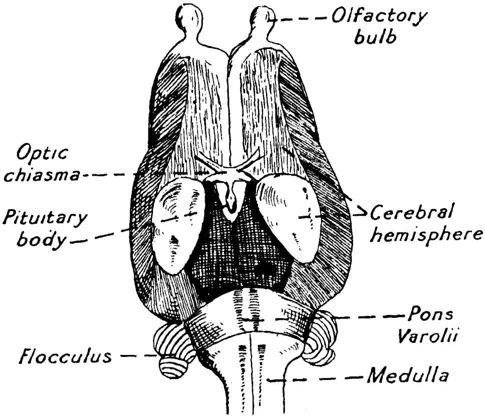


FIG. 134.—*Lepus.* Ventral view of brain.

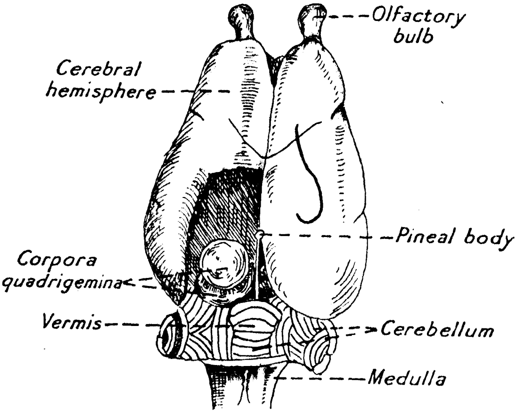


FIG. 135.—*Lepus.* Dorsal view of brain. Part of the roof of the left cerebral hemisphere has been removed.

The side walls of the diencephalon are very thick, forming the **optic thalami.** These are in contact in the centre, forming the so-called "soft commissure," thus constricting the cavity of the third ventricle. The floor of this part of the brain bears the

infundibulum, associated with the **hypophysis** to form the **pituitary body,** whilst from the roof projects the **pineal stalk.** On either side of the infundibulum is a band of longitudinal fibres, these bands constituting the **crura cerebri.**

Whereas the roof of the mesencephalon of the frog is thickened and expanded to form only two optic lobes these organs have each become divided into two in the mammal, the resultant structures being known as the **corpora quadrigemina.** The nerves from these structures pass forwards to cross beneath the floor of the hind end of the telencephalon as the **optic chiasma.** The side walls of the mesencephalon are formed by the crura cerebri.

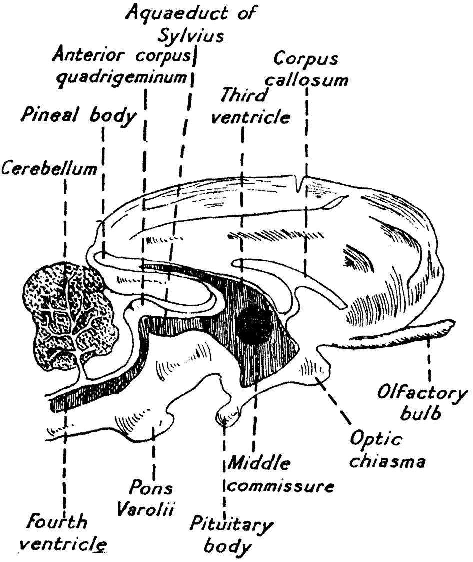


FIG. 136.—*Lepus.* Longitudinal section of brain.

In the metencephalon the **cerebellum** has become enlarged and subdivided into a median **vermis** and two lateral lobes. To the outer side of each lateral lobe occurs a small **flocculus.** The superficial layer (cortex) of the two sides of the cerebellum is connected by a band of transverse fibres, passing ventral to the rest of the brain and known as the **pons Varolii.**

The myelencephalon or **medulla** oblongata gradually narrows posteriorly to pass into the spinal cord.

The cavities of the brain are named as for the frog (page 153). The lateral ventricles each communicate with the cavity of the diencephalon (third ventricle) by a foramen of Monro. The cerebellum itself is solid, for the cavity of the fourth ventricle does not extend into it.

The brain is enclosed in membranes, collectively known as the **meningeal membranes.** The innermost is the **pia mater,** which is richly vascularised and penetrates the ventricles to form in the roof of each a **choroid plexus.** This membrane is enclosed in a protective **dura mater.** The space enclosed between these membranes and the brain is in communication with the cavity of the brain itself by a minute **foramen** of **Magendie** in the roof of the fourth ventricle.

(B) SPINAL CORD. The structure of the spinal cord is fundamentally similar to that of the frog described on page 153 and more fully discussed in Chapter XXIII.

(C) CRANIAL NERVES. There are twelve pairs of cranial nerves in the rabbit. The first ten pairs are similar in name and distribution to those of the frog. The eleventh pair is the **spinal accessory,** supplying muscles of the neck. The twelfth pair of nerves corresponds to the first pair of spinal nerves of the frog in distribution, and each is thus called an **hypoglossal.** It is only in the neck that the distribution of cranial nerves in the frog differs essentially from that of the rabbit. The vagus emerges through the foramen lacerum posterius and becomes expanded to form a vagus ganglion.

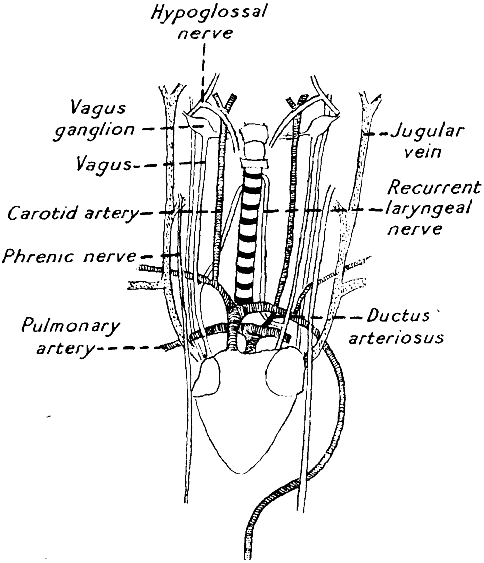


FIG. 137.—*Lepus.* Nerves of the neck.

Soon after this ganglion it gives off a **depressor** branch to the heart and an **anterior laryngeal** to the larynx. The main branch of the vagus passes ventral to the aortic arch on the left and to the innominate artery on the right. Each vagus then gives off a **recurrent laryngeal** nerve. The right recurrent laryngeal loops round the innominate artery, and that of the left side round the ductus arteriosus, each to run forwards to the larynx. The main branch of the vagus supplies the viscera. The hypoglossal (XII) passes on either side posterior to the angle of the jaw and sends backwards a **ramus descendens** to muscles of the neck.

(D) SPINAL NERVES. These are built on essentially the same plan as in *Rana*, but are, of course, much more numerous. The fourth and fifth cervical spinal nerves unite on each side to form a **phrenic** nerve to the diaphragm.

(E) SYMPATHETIC NERVOUS SYSTEM. Running on either side of the aorta is a ganglionated sympathetic nerve-cord. At each ganglion it receives a ramus communicans from the spinal nerve of that segment. It passes forwards, and in the hind end of the neck swells to form a posterior cervical ganglion. Dorsal to the vagus ganglion the sympathetic nerve-cord bears an anterior cervical ganglion, from which it continues forwards in company with the internal carotid artery. At the roots of both the anterior and the posterior mesenteric arteries is a ganglion, supplied with nerve fibres from neighbouring sympathetic ganglia. These mesenteric ganglia in turn innervate the musculature of much of the viscera, including the gut and the bladder. The collection of nerves centred around the anterior mesenteric artery forms the solar plexus.

Sense Organs. The sense organs of the rabbit differ from those of the frog only in detail. The ear is peculiar in that the cochlea is well developed, being in the form of a long, spirally-coiled tube. It is this part of the ear which accommodates the actual function of hearing, the remainder being concerned with balance. The whole ear is sunk deep into the head, and is in connexion with the tympanum by a chain of three ear-ossicles, through which vibrations are transmitted. The eye shows no distinction in structure from that of *Rana*, but both the lids are movable.

Cœlomic Cavity. The whole of the viscera is suspended by a dorsal mesentery in the spacious cœlomic cavity or splanchnocœl. The posterior part, known as the peritoneum, is separated from the anterior region by a transverse partition—the diaphragm. The anterior portion itself is further subdivided into a pericardial chamber, containing the heart, and two pleural cavities, in each of which is lodged a lung.

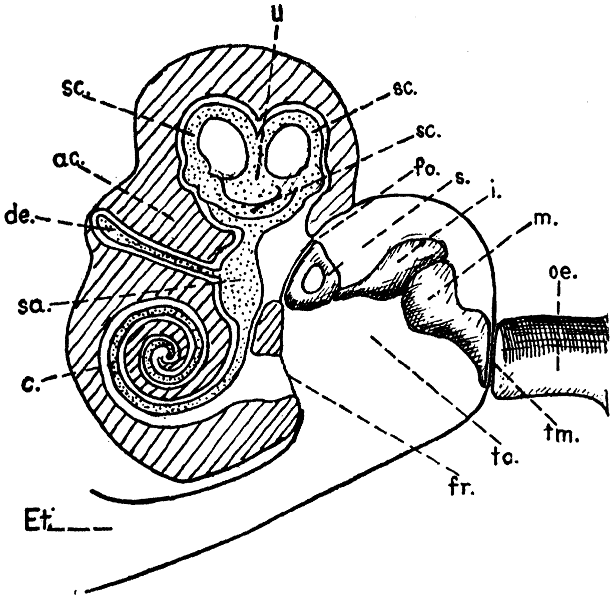


Fig. 138.—Diagram showing structure of mammalian ear. (From "Vertebrate Zoology," by G. R. de Beer.)

ac., auditory capsule; *c.*, cochlea; *de.*, ductus endolymphaticus; *Et.*, Eustachian tube; *fo.*, fenestra ovalis; *fr.*, fenestra rotunda; *i.*, incus; *m.*, malleus; *œ.*, external auditory meatus (outer ear); *s.*, stapes; *sa.*, sacculus; *sc.*, semi-circular canal; *tc.*, tympanic cavity; *tm.*, tympanic membrane; *u*, utriculus.

Urino-genital System. As with the frog the same organs are to some extent concerned both with excretion and with the evacuation of genital products, so that it is convenient to include them in one composite system. In both sexes the kidneys are asymmetric in position, the right one occurring some distance in front of the left. From the centre of each a **ureter** conveys urine back to the urinary bladder.

(A) Male. The testes are a pair of small, rounded, oval bodies, arising within the body-cavity, but later passing into a pair of **scrotal sacs** lateral to the penis. The path taken by each testis is indicated by a slender **spermatic cord,** composed of connective tissue and containing the spermatic artery and vein. Each testis is partly enclosed in a mass of coiled tubes, known as the **epididymis,** connected with the wall of the scrotal sac by a band of connective tissue, known as the **gubernaculum.** From each epididymis there passes forwards a **vas deferens,** which loops over the ureter to open into a median sac, known as the **uterus masculinus** and opening into the dorsal side of the neck of the bladder. The conjoined urinogenital duct is known as the **urethra,** communicating with the

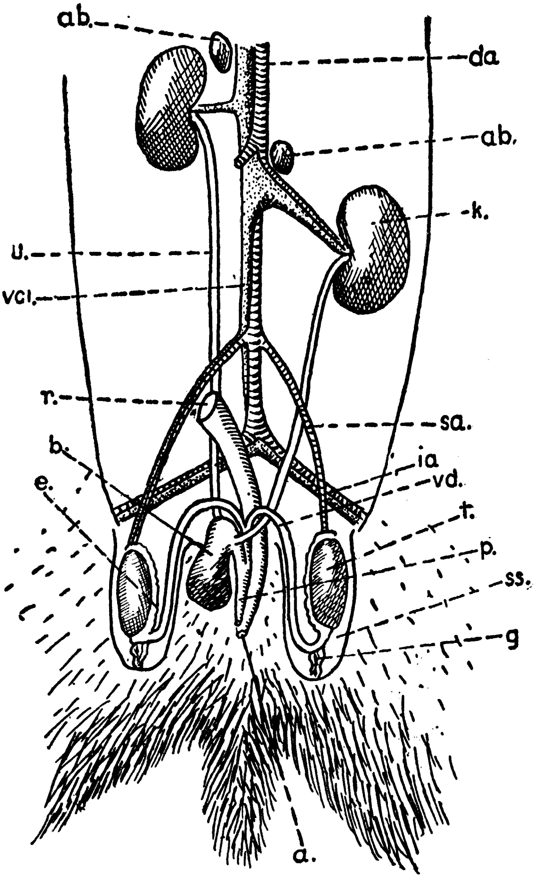


Fig. 139.—*Lepus.* Male urino-genital system. (From "Vertebrate Zoology," by G. R. de Beer.)

a., anus; *ab.*, adrenal body; *b.*, bladder; *da,* dorsal aorta; *e.*, epididymis; *g,* gubernaculum; *ia,* iliac artery; *k.*, kidney; *o.*, ovary; *oa.*, ovarian artery; *od.*, oviduct; *p.*, penis; *r.*, rectum; *ra.*, renal artery; *sa.*, spermatic cord; *ss.*, scrotal sac; *t.*, testis; *u.*, ureter; *ut.*, uterus; *v.*, vestibule; *va.*, vagina; *vci.*, inferior vena cava; *vd.*, vas deferens.

exterior by a muscular **penis.** Into either side of the uterus masculinus opens anteriorly a **prostate gland** and posteriorly a **Cowper's gland.**

(B) Female. In contrast to those of the frog the ovaries of the rabbit are very small, since there is little or no yolk in the eggs to which they give rise. There is a single ovary attached behind each kidney, and every egg is enclosed in a small sac, known as a **Graafian follicle.** Near each ovary lies the opening of an oviduct.

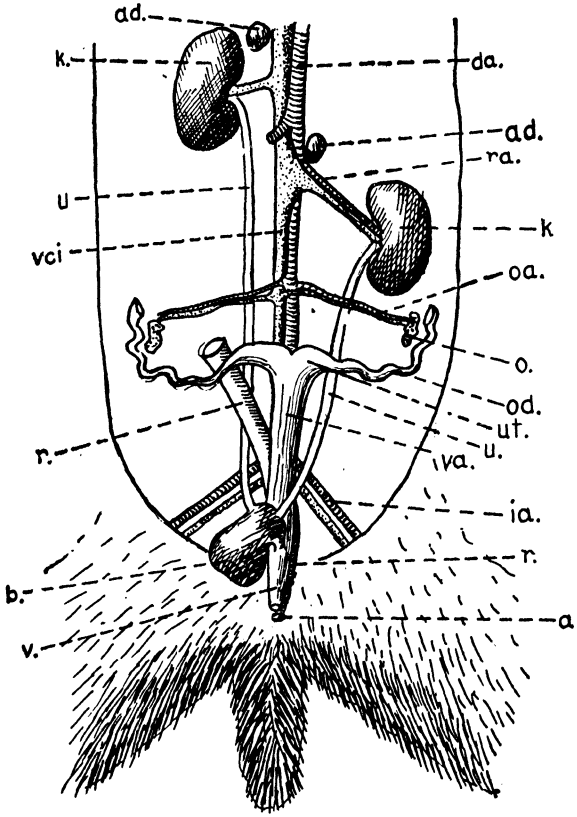


FIG. 140.—*Lepus.* Female urino-genital system. (From "Vertebrate Zoology," by G. R. de Beer.)
Key beneath Fig. 139.

Into these eggs are discharged when follicles burst. The first part of the oviduct is narrow and slightly twisted, leading into a wider, muscular part, known as the **uterus,** where early development of the embryos occurs. The two uteri unite to form a median **vagina,** opening posteriorly into the neck of the urinary bladder to form a conjoined urino-genital duct, or **vestibule,** opening to the exterior by the **vulva.** On the ventral wall of the vestibule lies a rod-like

clitoris, representing the penis of the male, whilst dorsally there occurs a pair of small **Cowper's glands.**

(C) REPRODUCTION. In spring the breeding season commences. At this time there is a periodic ripening of eggs. When ripe they are shed into the oviducal funnels and make their way to the uterus. This phenomenon is known as **ovulation,** taking place spontaneously when copulation (coition) occurs. In this event sperms are injected into the body of the female by the male, the penis becoming erected by an increase of blood-pressure and then being inserted into the vulva. The sperms swim up the vestibule in the fluid lining its walls, and one eventually fuses with each ovum present. Development then takes place within the uteri, each embryo becoming attached by a stalk or **umbilical cord,** along which nourishment is conveyed to the **fœtus** (developing embryo). After rather less than a month development is completed, this interval being known as the period of **gestation.** The process of parturition then occurs, the young organism being forced to the exterior through the vulva by the contraction of the walls of the uteri and vestibule. This type of reproduction, wherein the young are retained within the body of the mother, is described as viviparous, as compared with the oviparous forms like that of the frog, involving the laying of eggs and their subsequent development in the outside world. In the case of mammals, even after birth, the young are nourished on a milky secretion produced in the mammary glands of the mother.

Ductless Glands. The principal ductless glands are the **thyroid, parathyroid, thymus, pituitary** and **adrenal.** The thyroid is a bilobed structure, contained in a cartilaginous capsule and lying dorsal to the larynx. The parathyroids are closely associated with the thyroid, whilst the pituitary occurs beneath the floor of the mesencephalon, lying in a depression in the floor of the skull, known as the **sella turcica**. The **islets of Langerhans** are microscopic patches of tissue embedded in the pancreas, whilst anterior to each kidney is a small **adrenal body**. The gonads, too, as well as elaborating genital products, act as ductless glands, as discussed in Chapter XXIX. In the pregnant female the burst Graafian follicle becomes a ductless gland, known as the **corpus luteum,** responsible for certain somatic changes accompanying pregnancy.

CHAPTER XVI

COLUMBA

EXTERNAL FEATURES AND SKELETON. MIGRATION

THE pigeon is a domesticated descendant of the Rock Dove, *Columba livia*, found extensively throughout most of Europe and Asia. It is a member of the class Aves, characterised by being warm-blooded Chordata, with the fore-limbs modified to form wings. The body is invested with a covering of feathers, and reproduction is effected by the laying of large, heavily-yolked eggs enclosed in a calcareous shell.

External Features. The pigeon is shaped so as to offer minimum resistance to the air during flight. The hind-limbs alone are used for progression on land, and it is interesting to note that, despite this bipedalism, the body is still in a horizontal position. The hind-legs bear at their extremities feet, covered only by a layer of horny scales of purely epidermal origin. There are four toes only on each foot. The first toe is normally directed backwards and the remaining three forwards, thus giving stability to the bird. Each toe ends in a pointed claw. At the anterior end of the animal is the mouth. This is bordered above and below by a horny beak, and teeth are entirely absent. On each side of the upper part of the beak, some distance from the tip, is perforated a nostril. Behind the beak, on either side of the head, is set an eye, having three movable eyelids, corresponding to the upper and lower lids and the nictitating membrane in mammals. Postero-ventral to each eye occurs the opening of a tube leading to the ear-drum, which is not flush with the surface, as in the frog, but which has become sunk into the head. At the posterior end of the body is the tail. This is merely a cluster of feathers and is not supported by any extension of the vertebral column, as is that of mammals. Just ventral to the tail is a slit-like orifice, known as a cloaca, since it receives both the alimentary canal and the urino-genital ducts. On the dorsal side of the tail is a **uropygial** gland, significant owing to the production of an oily secretion with which the pigeon preens its feathers, rendering them water-proof. This is the only gland found in the skin of birds, a contrast to the possession of several types by the mammalian skin.

Feathers. The most significant of the external features of the pigeon is the possession of feathers. These are arranged in definite tracts or **pterylæ.** Considering first the adult bird there are essentially two types of feather, namely those visible on the outer surface and known as **pennæ,** and the down-feathers, forming a non-conducting layer near the surface of the body and known as **plumulæ.** The feathers of the adult bird are collectively known as the **teleoptiles.**

The pennæ include the flight-feathers of the wings and the contour-feathers of the body. Each consists of a central shaft or **rachis,** bearing a large number of processes or **barbs,** which together constitute the **vane.** Each barb is itself branched, bearing on each side a number of hooked **barbules.** It is by means of these hooked barbules that attachment between neighbouring barbs is effected thus imparting rigidity to the vane as a whole. There are two kinds of flight-feathers, the **remiges** of the wing and the **retrices** of the tail. The former are further subdivided into primary and secondary, the primary ones being borne on the carpals, metacarpals and phalanges, and the secondary on the radius and ulna. Contour-feathers may be distinguished from flight-feathers by the fact that they are smaller and their barbules are not so well developed. Furthermore they frequently possess an after-shaft. This is like a miniature feather arising from the posterior end of the rachis and on the dorsal side. The rachis itself is hollow and at its barbless end opens to the exterior by an inferior umbilicus below and a superior umbilicus above.

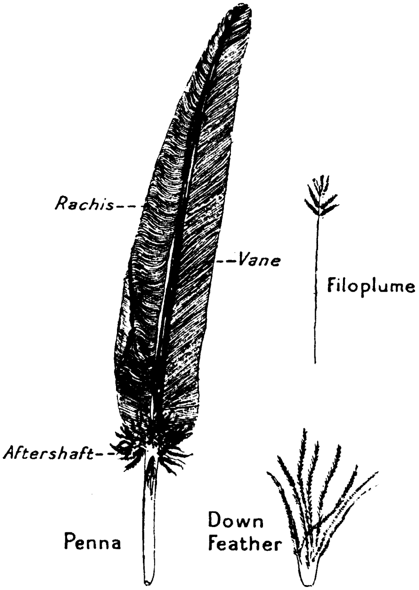


Fig. 141.—*Columba.* Types of feather.

The down-feathers or plumulæ are small and their barbules very degenerate. In some cases so marked is this degeneracy that there is little left of the feathers but the rachis. Such a structure is distinguished by the name of **filoplume.**

All these types of feather, collectively constituting the **teleoptiles,** are preceded in the young bird by nestling-feathers, or **neossoptiles,** smaller and softer than those of the adult. They are, nevertheless, differentiated into **prepennæ, preplumulæ** and **prefiloplumes,** giving place to the corresponding feathers of the adult.

Coloration of feathers is due partly to pigmentation and partly to interference owing to their surface-texture. It is commonly found that the plumage of the female is much more sombre than that of the male of its species, a phenomenon of protective significance, for it is normally the female that incubates the eggs and at this period she is thus rendered less conspicuous. Periodic moulting of feathers occurs, doing so more or less symmetrically in the case of the pennæ, so that flight is not impaired at such a season.

Skeleton. As with the frog and rabbit the various parts of the skeleton will be considered individually. One general feature may well be mentioned here. Many of the bones comprising the skeleton of the pigeon are very light, owing to the fact that air-cavities extend into them. This is manifestly an adaptation to the pigeon's habit of flying.

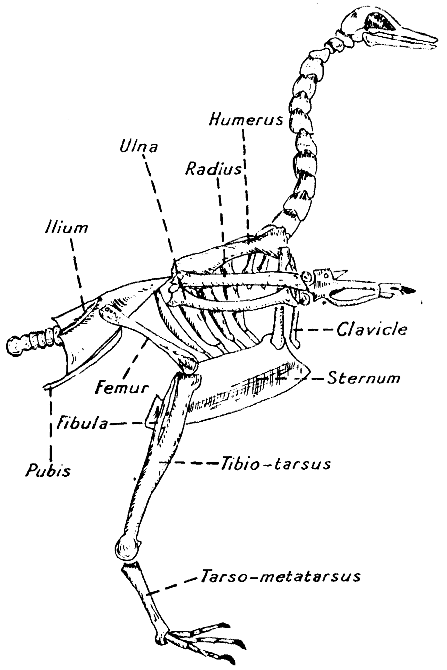


FIG. 142.—*Columba.* Right side of skeleton.

(A) SKULL. The skull of the pigeon is so richly supplied with dermal bones that compression between them tends to obliterate all sutures, which are so readily visible in the skull of the dog, for example. The neurocranium, comprised of cranium and sense capsules, is completely enclosed in bone. The roof consists, from the posterior end forwards, of **basioccipital, exoccipital, supra-occipital, parietals, frontals, prefrontals** and **nasals,** whilst each side is made up of **pleurosphenoid, squamosal** and **orbitosphenoid.** The floor consists of **basisphenoid** and **presphenoid.** The cranial cavity does not extend forwards between the eyes, for these are separated only by an interorbital septum, formed by fusion of the **mesethmoid** with parts of the presphenoid and orbitosphenoid. This septum is thickened along its ventral edge, forming the **rostral** bone. This corresponds to the blade of the parasphenoid in the skull of the frog, whilst posteriorly the cross-piece of the hilt of this latter bone is represented by a pair of **basitemporals,** one beneath each side of the basisphenoid. All the bones of each auditory capsule have become fused to form a **periotic,** whilst the **squamosal** bears a distinct **zygomatic process.** The **quadrate** is in connexion with the periotic by means of an **otic process,** whilst from the quadrate two narrow rods of bone project forwards on each side. The outer rod is the margin of the upper jaw, consisting from in front backwards of **premaxilla, maxilla, jugal** and **quadrato-jugal.** The inner rod consists of a **pterygoid** behind, running forwards to articulate anteriorly with both the **basipterygoid process** of the basisphenoid and the front end of the maxilla. A pair of **prevomers,** fused in the middle line, occurs between the anterior ends of the maxillæ. There is a single, median occipital condyle at the base of the skull.

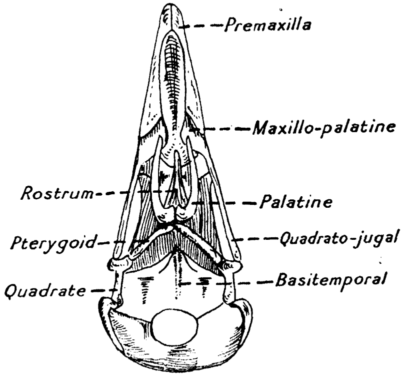


FIG. 143.—*Columba.* Ventral view of skull.

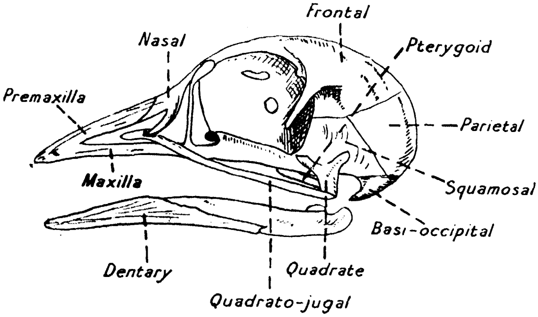


FIG. 144.—*Columba.* Lateral view of skull.

The lower jaw consists of only one cartilage-bone, the **articular,** representing the Meckel's cartilage of lower forms. Plastered on to the surface is a number of membrane-bones. These are the **angular, supra-angular, splenial** and **dentary** bone.

Connecting the tympanum with the fenestra ovalis is a slender **columella auris,** whilst ventrally the hyoid apparatus occurs in the form of a slender, forked bone, representing the basi- and cerato-hyal and -branchial elements of the first branchial arch of lower forms.

The following table will serve to summarise the bones of the skull of the pigeon :—

Bones Comprising the Skull

Region of Skull	Cartilage-bones	Membrane-bones
Roof	Exoccipital Basioccipital	Supraoccipital Parietals Frontals Prefrontals Nasals
Side wall	Pleurosphenoid Orbitosphenoid	Squamosal
Internasal septum	Mesethmoid Presphenoid Orbitosphenoid Rostrum	
Floor	Basisphenoid Presphenoid Basitemporals	Vomer
Auditory capsule	Periotic	
Upper jaw and associated bones		Premaxilla Maxilla Jugal Quadrato-jugal Palatine Pterygoid
Lower jaw	Articular (articulates with the quadrate)	Dentary Splenial Angular Supra-angular

(B) Vertebral Column. The regional differentiation of the vertebral column is much like that of *Lepus.* Thus the first part is the cervical region.

(i) *Cervical Region.* This consists of fourteen vertebræ, the first two of which are the atlas and axis respectively, modified similarly to the corresponding structures in the rabbit. The vertebræ in this region are of a peculiar shape, and are described as **heterocœlous,** In front each is laterally concave and dorso-ventrally convex, whilst posteriorly these curvatures are reversed. In this way greater flexibility is imparted to the neck. The first two vertebræ have no ribs, whilst the next ten have ribs fused by a double head to the centrum and transverse process on either side. Thus a vertebrarterial canal is enclosed, as in the rabbit. The last two cervical vertebræ have ribs articulating freely, but ventrally even these do not reach the sternum.

(ii) *Thoracic Region.* There are only five thoracic vertebræ, the first four of which are fused together and the fifth to the first lumbar. Each of these vertebræ bears a pair of ribs, attached ventrally to the sternum. The free ribs of this and the cervical region, excepting the last pair of thoracics, all bear uncinate processes, which overlap considerably, thus strengthening the wall of the thorax.

(iii) *Lumbar Region.* There are six lumbar vertebræ, themselves fused together, and fused in front with the last thoracic and behind with the two fused sacral vertebræ and the first five fused caudals. In this manner a very strong sacrum is formed for the attachment of the ilia of the pelvic girdle.

(iv) *Sacral Region.* As already indicated, this consists of two vertebræ fused together.

(v) *Caudal Region.* Behind the first five, which are fused, there are found six free caudal vertebræ, followed in turn by four more, fused together to form a pygostyle.

(C) STERNUM. The sternum is a broad plate of bone lying ventrally in the body-wall. Posteriorly it bears a large, median keel or **carina** for the attachment of muscles, the **pectoralis major** and the **pectoralis minor,** used for the lowering and raising of the wings respectively. According to the extent to which these muscles are used, the "breast" of a bird may be "red" or "white" meat.

(D) PECTORAL GIRDLE AND FORE-LIMB. The pectoral girdle is formed on each side by stout **scapula** and **coracoid** and slender **clavicle.** The scapula lies over the ribs, directed backwards, whilst the coracoid connects its anterior end with the sternum. The clavicle meets the corresponding bone from the other side to join with it in the middle line. At the junction of the scapula, coracoid and clavicle on each side is enclosed a **foramen triosseum,** through which passes the tendon of the pectoralis minor muscle.

The skeleton of the wing consists of a short, stout **humerus,** articulating proximally with the coracoid and distally with the **radius** and **ulna.** These latter bones remain completely separate, being merely in contact at their extremities. The wrist consists of two free proximal carpals, the **radiale** and the **ulnare**, whilst distally the carpals have become fused with three metacarpals to form a **carpo-metacarpus.** The two principal digits bear two and one phalanges respectively, whilst the first digit consists only of a phalanx, bearing a number of feathers.

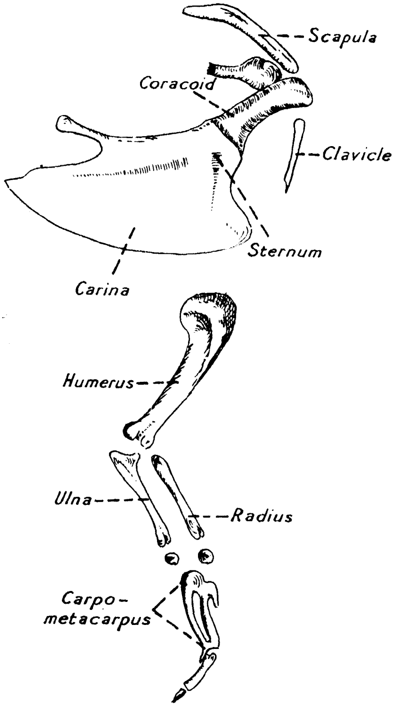


FIG. 145.—*Columba.* Pectoral girdle and fore-limb.

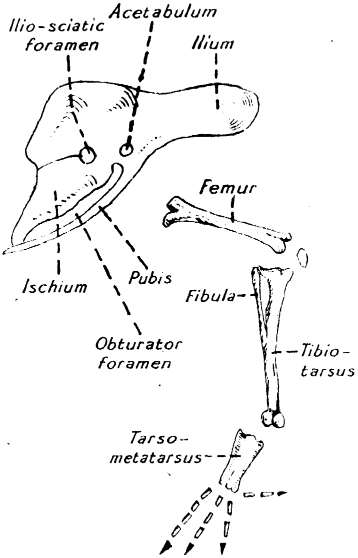


FIG. 146.—*Columba.* Pelvic girdle and hind-limb.

(E) PELVIC GIRDLE AND HIND-LIMB. The pelvic girdle consists of two plates of bone, one ventro-lateral to each side of the sacrum. It is made up of an **ilium** extending along the entire length of the sacrum, whilst the **ischium** is fused with the postero-ventral corner of the ilium, enclosing an **ilio-sciatic foramen,** through which the sciatic artery and nerve pass to the leg. The **pubis** is a slender bone running backwards, parallel to the ventral border of the ischium, with which it is fused. Between the pubis and ischium is a narrow **obturator fissure,** corresponding to the obturator foramen of *Lepus.* The **acetabulum,** into which fits the head of the femur, is completely perforated, and all three bones of the girdle contribute to its limiting wall. The two halves of the girdle do not extend into the midventral line, so that no symphyses are formed.

The **femur** is a short, stout bone, articulating distally with the **tibia.** This latter is not a single bone, but laterally there occurs a slender **fibula,** fused to the tibia at about the middle of the length of the latter and free only at its proximal end. The joint between the femur and tibio-tarsus (see below) is covered by the **patella.** To the distal end of the tibia are fused the proximal tarsals, the whole structure being known as the **tibio-tarsus.** Similarly the distal tarsals are fused with the metatarsals of the second, third and fourth digits, forming the **tarso-metatarsus,** whilst the first metatarsal remains free ; there is no fifth digit present. The first four digits bear respectively two, three, four and five phalanges.

Running in all the digits are tendons, serving to bend them. The tendons pass up behind the joint between the tibio-tarsus and the femur. Thus when a bird is roosting the bending of the legs in the assumption of a squatting position results in these tendons being pulled, and thus the toes are tightly drawn around its perch.

Migration

One of the most characteristic features of the mode of life of many birds is the habit of travelling from one region to another at certain seasons of the year. The journey may be comparatively long or short. Thus the swallow flies from the British Isles to Mediterranean countries in autumn and returns in spring, whilst the curlew at similar seasons travels between moorland and the seashore. The whole phenomenon may best be understood by the selection of an example and the tracing of events throughout a complete annual cycle. The swallow will be chosen for this purpose.

During the winter males and females, young and old, live a communal life, building no nests and seeking shelter wherever it can be obtained. The song is but poorly developed and serves only to guide other members of the species to food or to divert them from danger.

With the advent of spring the males first depart for the British Isles. On arrival each seeks out a site suitable for the subsequent construction of a nest. This it defends, and is then said to have " acquired a territory." This done, the call-note characteristic of the breeding season is developed. Some fortnight later the females arrive, and each mates with a male which has acquired a territory. Together they build a nest. Copulation occurs, eggs are laid and then hatched. A certain amount of parental attention is paid to the fledglings, and eventually they are able to fly and fend for themselves.

In the following autumn young and old alike collect together into droves and return to their winter quarters.

In explanation of this phenomenon it must be assumed that the whole sequence of events is controlled from the **corpus striatum** of the bird, where the particular arrangement of the nerve cells causing the various actions to follow each other in regular succession is as much a part of the inherited constitution of the bird as, say, the colour of the plumage. The completion of each single event in the chain affords the stimulus for the commencement of the next. The beginning of activity in spring may well be due to the direct effect of change in climatic conditions on the gonads.

The obvious result of this migratory habit is that a continual selection of members of the race is being effected, for only the fittest can survive. Each stage is itself a severe test for a bird of its size, more especially the migratory flights.

CHAPTER XVII

EMBRYOLOGY OF AMPHIOXUS

THE egg commences to develop almost at once after fertilisation, its symmetry having already been determined, the antero-posterior axis by the position of attachment of the egg in the ovary and the dorso-ventral by the point of entry of the sperm.

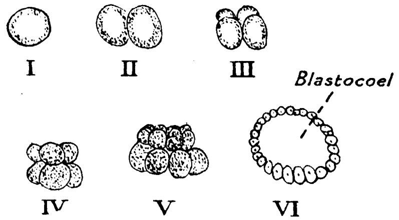


FIG. 147.—*Amphioxus.* Cleavage of egg to blastula stage.

Cleavage. There is little yolk present in the egg of *Amphioxus,* so that cytoplasmic cleavage can keep pace with nuclear division. Such cleavage is said to be total or **holoblastic.** As a result of cleavage a solid ball of cells, known as a **morula,** is formed, and later this becomes hollow to form a **blastula,** the cavity of which is known as a **blastocœl.** The cells at the posterior end are larger than those at the anterior end, and the wall of the entire structure is but one cell thick.

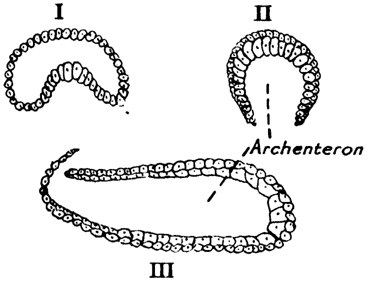


FIG. 148.—*Amphioxus.* Formation of gastrula.

I and II. Transverse section.
III. Longitudinal section.

Gastrulation. The posterior end of the blastula now becomes flattened, and soon is seen to be becoming invaginated towards the anterior wall, thus reducing the size of the blastocœl. As a result of this process a new cavity is formed, known as the **archenteron,** bordered by a double wall, the inner layer of which is known as the **endoderm** and the outer as the **ectoderm.** It is in communication with the exterior by a minute **blastopore.** The lips of the blastopore grow posteriorly, thereby increasing the length of the gastrula as this stage is called. This process of growth by the rim of the blastopore is known as **epiboly.** The endoderm and ectoderm thus formed are known as germ-layers, for all the organs of the future adult are derived from them. There is formed at a later stage a third layer, known as the **mesoderm** and situated between the endoderm and the ectoderm. Though also described as a germ-layer, it is in reality derived from the endoderm.

Formation of Nerve-cord. The nerve-cord arises from the ectoderm. A layer of cells along its dorsal surface becomes flattened to form the **neural plate.** It sinks in somewhat along the middle line and a neural fold arises on either side. The two folds eventually meet and coalesce dorsally, so that in this way an hollow tube is formed. The outer layer of ectoderm above this tube closes over. Only at the extreme anterior end do the neural folds fail to meet, so that in this region an aperture is left, represented in the adult by **Kolliker's pit.** At the posterior end, on the other hand, the neural folds come to roof over the blastopore, which now communicates only with the cavity of the nerve-cord and not with the exterior. This opening between the nerve-cord and the archenteron is known as the **neurenteric canal.**

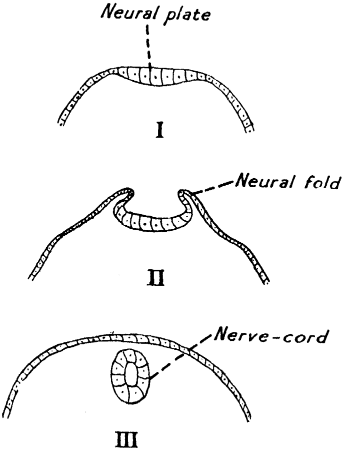


FIG. 149.—*Amphioxus.* Formation of nerve-cord.

Formation of Notochord. Along the dorsal surface of the endoderm, beneath the nerve-cord, a rod of cells soon becomes specialised to form a solid notochord. As the animal increases in length new material is added to the notochord by cell-division at the dorsal lip of the blastopore.

Formation of Mesoderm. The mesoderm is formed from a portion of the endoderm on either side of that giving rise to the notochord. On each side a process of evagination occurs, thus forming a pair of longitudinal folds which extend upwards for some distance, but retain their openings into the archenteron below. At this point a transverse partition arises, cutting off a small, anterior portion from the remainder of each fold posteriorly. The bases of these anterior folds now become completely constricted, so that in this way a pair of somites is formed, cut off from the cavity of the archenteron laterally and from the remainder of the mesodermal folds posteriorly. Eventually the remainder of each fold becomes nipped off completely from the archenteron progressively from in front backwards, and following this separation the tube thus formed on each side becomes divided up into somites by the laying down of transverse partitions. This is in contrast to the first pair of somites, which become separated from the remainder of the mesoderm before being cut off from the cavity of the archenteron. But it will be remembered that the fully formed gastrula was produced partly by invagination and partly by epiboly. The mesoderm derived from the endoderm formed by invagination—i.e. the anterior part of the mesoderm—is described as **gastral,** whilst that developed from endoderm formed as a result of epiboly—i.e. the more posterior mesoderm—is described as **peristomial.**

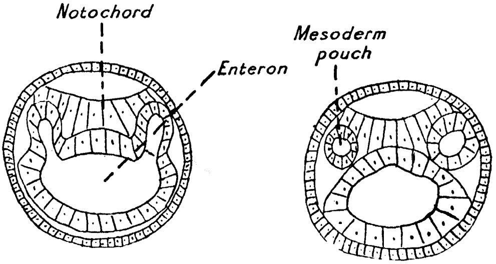


FIG. 150.—*Amphioxus.* Formation of mesoderm pouches and notochord. Transverse section.

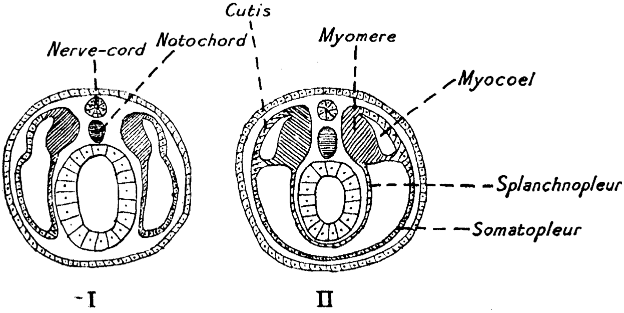


FIG. 151.—*Amphioxus.* Ventral extension of mesoderm. Transverse sections.

The mesodermal somites now commence to extend ventrally, running between the gut-wall and the ectoderm. Eventually each meets the corresponding structure from the other side in the mid-ventral line, and there their separating walls are absorbed. Thus each pair of somites forms a hoop of hollow mesoderm extending ventrally beneath the gut. The cavity between the two layers of mesoderm is the **cœlom,** whilst the mesodermal walls of this cavity constitute the cœlomic epithelium. The epithelium lying against the endoderm is known as the splanchnic layer or **splanchnopleur,** whilst that against the ectoderm is the somatic layer or **somatopleur.** The original pouches—i.e. those parts of the mesoderm formed prior to their ventral extension round the gut—become further differentiated. Their cavities are known as **myocœls,** and become separated from the cavities (**splanchnocœls**) of the ventral parts by transverse partitions. The inner wall of each mycocœl, lying against the nerve-cord and notochord, becomes much thickened to form a muscle-block or **myomere,** whereas its outer wall becomes the cutis immediately beneath the ectoderm. The myocœls retain their segmental arrangement, but the septa between the splanchnocœls break down, so that ventrally a continuous, perivisceral cœlom is formed, enclosing the gut throughout its entire length. The myomeres, at first regular, soon become V-shaped and alternate on right and left sides.

As well as the mesodermal cavities already described, there arises from the anterior end of the endoderm a pair of head-cavities, peculiar on account of their asymmetry. Though of symmetrical origin, the right one soon becomes very much enlarged, whilst the left one establishes a communication with the base of an ectodermal inpushing, known as the preoral pit, and there opens to the exterior. In the adult this is represented by Hatschek's pit.

Only one other feature in connexion with the development of mesoderm is important, and that is the formation of the gonads. In the anterior part of the body a downgrowth from each myocœl gives rise to a **gonocœl,** and these two new cavities constitute the gonads, their walls being the germinal epithelium.

Alimentary Canal. The mouth is perforated at the anterior end of the body and to the left of the middle line. It becomes ciliated. The neurenteric canal now becomes closed and the anus is perforated just beneath it. Meanwhile the splanchnopleur is becoming modified to form a coat of involuntary muscle surrounding the gut, and the liver diverticulum arises from the right side of the gut.

But it is principally the pharynx which is important at the moment, owing to the rather peculiar manner in which the gill-slits are formed. The first structure to be formed in this region is not a gill-slit at all, but is the so-called **club-shaped gland.** It arises as a diverticulum from the anterior end of the gut, into which it opens on the right side, whilst it perforates the ectoderm to open on to the surface a little to the left of the midventral line. The gill-slits of the left side are perforated before those of the right. Each is formed by an endodermal evagination and an ectodermal invagination, the two meeting and their walls being absorbed over the region of contact. It follows that the wall of each slit is partly ectodermal and partly endodermal in origin. The first gill-slit of the left side arises in this manner in the midventral line and subsequently moves up the right side of the body. Some dozen gill-slits are formed behind this one in a precisely similar manner, and thus arise what are known as the primary gill-slits. The gill-slits of the right side, known as the secondary gill-slits, arise dorsal to those already present. They are only eight in number, and the most anterior secondary lies immediately above the second primary. This apparent anomaly is explained by the assumption that the club-shaped gland, mentioned above, is morphologically the first secondary gill-slit.

Whilst still occupying this curious position the two sets of gill-slits become separated by a rudimentary endostyle. This originates in front of the club-shaped gland and then extends backwards between the primary and secondary gill-slits, becoming differentiated to show the typical structure of the adult as it elongates.

At this point a more reasonable symmetry is developed, for the two lots of gill-slits and the endostyle start to move in a ventral direction. This movement stops only when the endostyle is in the midventral line and the primary gill-slits on the left side more or less correspond in position to the secondary slits on the right. At the same time the mouth becomes reduced in size, and its original margin is drawn in on all sides to form the velum. This simplicity of arrangement of the gill-slits does not persist for long, for a great deal of subdivision takes place by the downgrowth of tongue-bars from the roofs of the original slits. Thus, as already pointed out, these tongue-bars do not contain any cœlomic cavity, for they are formed by the subdivision of structures which pass through the cœlom, but which are not part of it. The primary gill-bars—i.e. the walls of the original gill-slits of the two sides prior to subdivision—do contain a portion of the cœlom, for the walls separating these slits are merely those regions of the body-wall which have not become interrupted by the perforation of gill-slits. The tongue-bars can no more contain cœlom than can the gill-slits themselves.

Atrium. It will be remembered that the gill-slits of *Amphioxus* do not open direct to the exterior, but into a portion of the outside world enclosed between the body-wall and the atrium. This latter arises in the form of a pair of longitudinal folds, known as **metapleurs,** one above the gill-slits on either side. Each fold grows in a ventral direction, and from it arises a shelf, known as an **epipleur,** extending towards the midventral line, where it meets and fuses with the corresponding structure of the other side, thus enclosing a space. The anterior walls become cemented down to the body-wall, and at the posterior end the cavity is in communication with the exterior by a small atriopore.

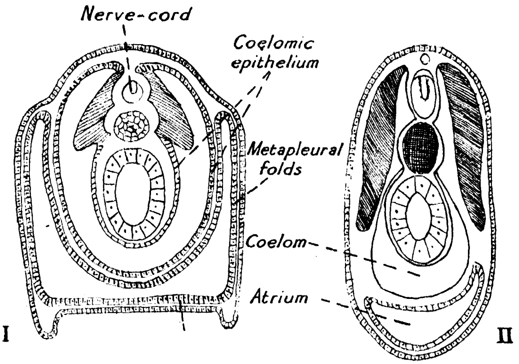


FIG. 152.—*Amphioxus.* Diagrams to show formation of atrium. Transverse sections.

Nephridia. The excretory organs of *Amphioxus* arise as small, blind outpushings at the top of the original gill-slits, prior to the formation of tongue-bars. Each extends for some distance down the cœlomic cavity of a primary gill-bar and opens to the exterior near the apex of the neighbouring tongue-bar. Flame-cells are developed as outgrowths from the tube. Hatschek's nephridium arises similarly as a small tube near the preoral pit, but instead of leading to the exterior it communicates with the pharynx of the adult.

The following table affords a summary of the various structures found in *Amphioxus* and indicates the germ-layer from which each is derived :—

ORIGIN OF STRUCTURES IN AMPHIOXUS

Ectoderm	Mesoderm	Endoderm
Epidermis	Dermis	Alimentary canal
Atrium	Myotomes	Liver
Nephridia	Blood-vessels	Endostyle
Wheel organ	Cœlom	Inner part of gill-bars
Outer part of gill-bars	Gonads	
Nerve-cord		Notochord

CHAPTER XVIII

EMBRYOLOGY OF RANA

UNLIKE the egg of *Amphioxus* that of *Rana* contains a considerable quantity of yolk. Furthermore it is enclosed within a mass of jelly-like material, wherein it can rotate. The vegetable pole, containing large quantities of yolk, comes to lie beneath the animal pole, which is itself deeply pigmented. Thus the future antero-posterior axis of the animal lies in a vertical plane. As with the egg of *Amphioxus*, bilateral symmetry is established with the entry of the fertilising sperm, for soon after fertilisation a lightish area appears in the cytoplasm diametrically opposite to the point of entry of the sperm. This area is known as the **grey crescent,** and marks the dorsal surface of the future organism.

Cleavage. Despite the presence of yolk, cleavage is still total—i.e. the rate of cytoplasmic cleavage keeps pace with that of nuclear division, and the whole egg takes part in this process of division (cf. the cleavage of the egg of *Gallus*, page 230). But the cells (**blastomeres**) thus produced differ greatly in size amongst themselves, those of the future posterior end being the larger, owing to their yolk-content. Eventually an hollow **blastula** is formed, differing from that of *Amphioxus* in that its wall is several cells thick. Since the cells of the vegetable pole are the larger it follows that the **blastocœl** lies nearer the animal pole.

Gastrulation and Formation of Mesoderm. The process whereby the blastula is converted into a two-layered **gastrula** is at first sight different from that of *Amphioxus*, but this discrepancy is apparent rather than real. It is the same process modified by the presence of yolk. Owing to their smaller size the cells of the animal pole divide more rapidly than those of the vegetable pole, and in fact begin to spread in a ventral direction over the latter. In the region of the grey crescent this overgrowing layer becomes tucked in to form the inception of the future **dorsal lip** of the **blastopore.** From this dorsal lip the rim of the blastopore becomes extended downwards on both sides, and soon these two lateral lips converge and fuse beneath the dorsal lip, so that the blastopore is now completely enclosed, whilst through it project yolk cells, forming the **yolk plug.** Since invagination occurs chiefly on the dorsal side of the embryo, yolk cells become displaced to the ventral side, so that the symmetry of the developing organism is upset. In consequence the whole rotates through an angle of 100°, thus bringing the antero-posterior axis to lie almost horizontal. As a result of invagination the original blastocœl is almost obliterated, being replaced by the gut-cavity or **archenteron.** The invaginated material forms the gut roof, from which the notochord and some of the mesoderm are eventually derived. The anterior end, floor and lateral walls of the gut are formed from yolk cells. The mesoderm is formed of tissue invaginated from the lateral and ventral lips of the blastopore in such a way that at one stage the endoderm and mesoderm take the form of two cups of tissue, their concavities facing each other and directed towards the centre of the incipient gastrula. The endoderm cup is situated at the anterior end of the embryo, with its concavity directed backwards and upwards. Facing it is the cup of mesodermal tissue, whose concavity is thus directed forwards and downwards. These two cups of tissue continue to grow at their margins, and eventually the endoderm forms an almost complete sphere within the sphere of mesoderm enclosing it. In this way the three primary germ-layers are formed. Later a split occurs in the mesoderm on either side, thus forming a rudimentary **cœlom**, the inner and outer walls being known respectively as the splanchnopleur and the somatopleur.

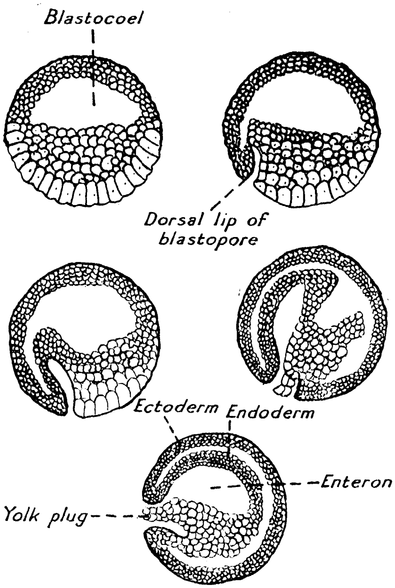


FIG. 153.—*Rana*. Process of gastrulation.

According to its origin the mesoderm, like that of *Amphioxus*, is either gastral or peristomial. If it is derived from endoderm formed as a result of the process of invagination it is described as gastral, whereas if it arises from endoderm produced by the passage backwards of the rim of the blastopore (i.e. epiboly) it is said to be peristomial. In structure these two kinds of mesoderm are identical.

Notochord. A rod of cells along the dorsal side of the endoderm marks the position of the future notochord, which is formed as a result of the complete separation of this rod from the roof of the archenteron. This separation is effected distinctly only anteriorly, whilst posteriorly the layers are less clearly demarcated, this culminating at the dorsal lip of the blastopore, where ectoderm, endoderm and mesoderm are all continuous.

Nerve-cord. Along the mid-dorsal line the ectoderm becomes flattened to form the **neural plate.** On either side of this arises a longitudinal fold. These extend dorsally and converge towards the middle line, where they fuse to form a tube. In this way the nerve-cord is formed, containing the neural canal. Posteriorly the neural folds grow round the blastopore, which still remains open to the exterior. The cavity of the nerve-cord communicates with the archenteron by the **neurenteric canal.** But the whole neural plate is not concerned with the formation of the nerve-cord, for a portion on either side gets carried up to lie at the dorso-lateral corner of this structure, where it forms a **neural crest,** later giving rise to the afferent fibres of the nerves which are in connexion with the nerve-cord.

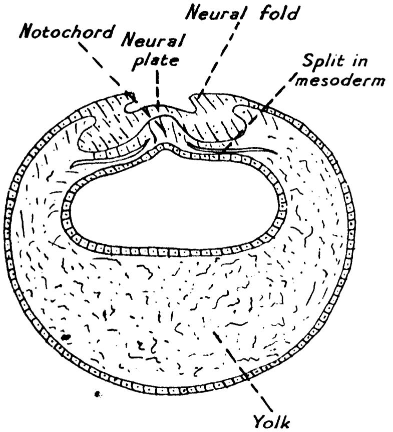


FIG. 154.—*Rana.* Transverse section, showing formation of nerve-cord, notochord and mesoderm.

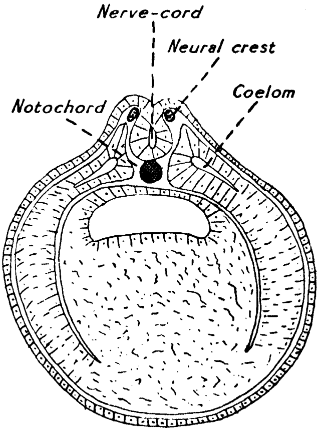


FIG. 155.—*Rana.* Transverse section, showing further formation of cœlom.

Segmentation. But as in *Amphioxus* the embryo later becomes divided transversely by septa into segments, this being more apparent in the case of the mesoderm. Again as in *Amphioxus* this process takes place only dorsally and proceeds from in front backwards. The inner wall of the mesoderm of this dorsal region becomes thickened to form the muscular coat of the body-wall, and each portion, separated transversely from that in front of and behind it, is a myomere. The portion of the mesoderm which becomes thus segmented is known as the **vertebral plate,** whilst the ventral, unsegmented region is the **lateral plate.** Connecting the two, and corresponding in position to each myotome on either side, is an intermediate cell-mass or **nephrotome.** Eventually the lateral plate becomes completely cut off from the vertebral plate, the musculature (myomeres) of which now extends ventrally to give rise to the muscles of the ventral part of the body-wall and of the limbs. Corresponding to each myomere arises a ventral root of a nerve (Chapter XXIII), whilst the neural crest also becomes segmented on a similar basis to form the dorsal roots. Thus muscles and nerves display the same metameric segmentation, and it is indeed from the latter that segmentation is sometimes betrayed where otherwise it has become almost completely obscure, as is the case with the vertebrate head.

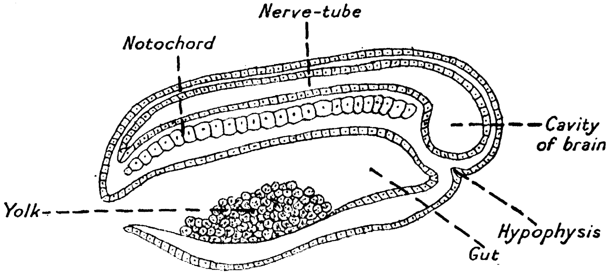


FIG. 156.—*Rana.* Longitudinal section to show formation of nerve-cord and notochord.

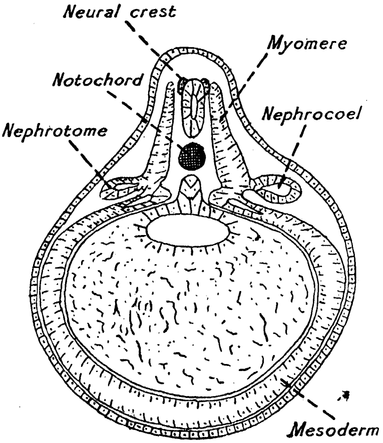


FIG. 157.—*Rana.* Transverse section, showing formation of nephrotome.

Since, as has been stated, the nerves are segmental in arrangement, it follows that the vertebræ must be of segmental origin, for they alternate regularly with the nerve-roots. They arise, in fact, from cells, known collectively as **mesenchyme,** budded off from the inner sides of the myomeres. These become arranged about the nerve-cord and notochord in the form of masses, termed **sclerotomes.**

Kidneys. The kidneys also are of segmental origin, arising from certain nephrotomes, mentioned above. On each side the nephrotomes of the second to fourth segments of the trunk become modified to form ciliated funnels, communicating with the cœlom. At their outer ends they are in connexion with a rod of cells which comes to extend backwards between the ectoderm and the somatopleur as far as the anus. Eventually this rod of cells becomes converted into a tube, opening into what now becomes a cloaca.

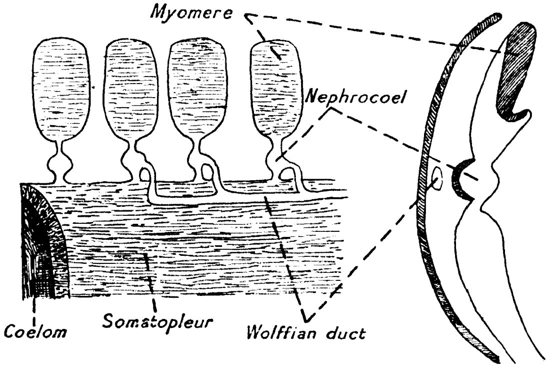


FIG. 158.—Diagram to show formation of kidney-tubules and Wolffian duct.
A. Side view. B. Transverse section.

Thus at this stage there is established a direct communication between the cœlom and the exterior through the cloaca. These cœlomic funnels (**cœlomostomes**) and associated tubules constitute what is known as the **pronephros,** and the tube connecting them as the pronephric duct. The pronephros itself becomes somewhat enlarged as the result of elongation of the tubules, whilst the cœlomostomes receive branches from the dorsal aorta and posterior cardinal vein, disposed by this time somewhat as in the dogfish. This structure remains as the functional kidney in the embryo and early larva, but later degenerates and disappears. It is replaced by the functional kidney of the adult, known as a **mesonephros.** This is formed from the nephrotomes of some six segments on either side, a little distance behind the pronephros. Cœlomostomes are formed, and the tubule of each grows outwards to open into the pronephric duct already present. From this point onwards it becomes known as the **Wolffian duct,** and loses its connexion with the pronephros. The tubules of the mesonephros become very much branched and their blind endings very much invaginated to form cup-shaped vesicles, known as **Bowman's capsules.** Into each extends a minute branch of the dorsal aorta and of a posterior cardinal vein, and within the capsule these break up to form a number of capillaries, known as a **glomerulus.** Bowman's capsule and glomerulus together constitute a **Malpighian corpuscle.** Thus blood for the hind end of the body is carried to the kidneys on its return journey to the heart, so that the posterior region of each posterior cardinal vein becomes the renal portal vein.

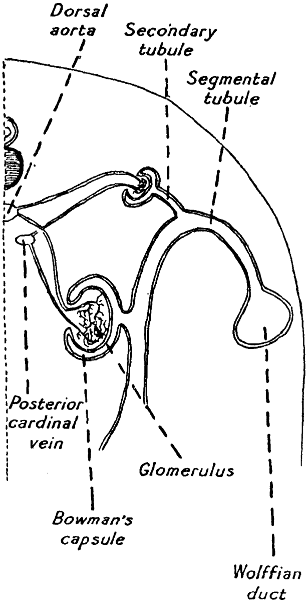


FIG. 159. — Diagrammatic transverse section to show formation of kidney.

Gonads and their Ducts. In close association with the kidneys are ducts of the gonads. The gonads themselves arise as evaginations of cœlomic epithelium at the dorso-median corners of the splanchnocœl. In these evaginations arise strands, containing the primordial germ-cells. In embryos destined to become males these strands become hollowed out and establish connexion with the tubules of the mesonephros. Thus the **vasa efferentia** are formed, and the spermatozoa produced later pass along these tubes to reach the exterior *viâ* the Wolffian duct.

But the eggs of the female are not passed along a ready-made duct, so that in this sex a pair of **Müllerian ducts** arises to act as oviducts. Each Müllerian duct originates in the form of a longitudinal groove in the wall of the cœlom to the outer side of the gonad. This groove becomes folded over to form a tube which communicates anteriorly with the cœlom just behind the region occupied by the pronephros of the early larva, whilst posteriorly it opens into the cloaca. The Müllerian ducts are represented in the male, but later degenerate and almost completely disappear.

Alimentary Canal. This is formed from the original archenteron and is completely closed in by endoderm. In the posterior part there is for a long time a collection of yolk cells. Gradually the whole becomes regionally differentiated to form the divisions characteristic of the adult, but in the earlier stages it is the perforation of the gill-slits in the pharyngeal region which is of primary importance. Five pairs of visceral clefts are formed by evagination of endoderm and slight invagination of the ectoderm opposite. The first pair of pouches represents the spiracles of *Scyllium*, but in the frog they never become perforated, though their cavities remain as the Eustachian tubes. The remaining four pairs eventually become perforated to form gill-slits. But respiration is first effected not by these true, internal gills, but by external gills, of which there are three pairs, arising as excrescences from the third, fourth and fifth visceral arches (i.e. the arches behind the first, second and third true gill-slits). They become richly vascularised. In this same region arise two important ductless glands. The thyroid is formed as a depression in the floor of the pharynx between the second gill-slits. It loses its connexion with the cavity of the mouth and pours its secretion into the blood. From the roof of the first gill-slit arises the thymus gland as a downgrowth, in the same way as does a tongue-bar from the primary gill-slits of *Amphioxus*. Thus the thymus gland is said to be homologous with the tongue-bars of *Amphioxus*. Posterior to the thyroid gland a ventral diverticulum of the pharynx gives rise to the larynx. This forks, and each free end becomes expanded to form a lung. The liver arises behind the larynx, also as a ventral diverticulum, and becomes enlarged and lobulated. It retains its connexion with the alimentary canal by the bile-duct, near the opening of which arises the pancreas as an outgrowth from the gut. Finally, a ventral diverticulum from the rectum becomes bi-lobed to form the urinary bladder.

The whole gut is suspended in the cœlom, being covered by the splanchnopleur except in the mid-dorsal line and separated from the somatopleur by the cœlomic cavity, containing cœlomic fluid. The wall of the cœlom in the region of the gut becomes known as the **peritoneum.** In the mid-dorsal line the inner walls of the cœlom become closely applied to form the dorsal mesentery. This mesentery becomes specially folded to support the various diverticula of the gut, as well as the heart and principal blood-vessels. The cœlomic cavity containing the heart becomes separated off by a transverse partition from the remainder of the cœlom in which the gut is suspended (perivisceral or peritoneal cavity). The chamber enclosing the heart is the **pericardium.**

Vascular System. A number of mesoderm cells between the floor of the gut and the splanchnopleur by which it is suspended become arranged in the form of a tube, known as the **subintestinal** vessel. The walls of this become thickened and its cavity subdivided, thus forming an heart. The dorsal aorta is of paired origin, the **lateral aortæ** which comprise it remaining separate in front in the form of the **carotid arches** and uniting posteriorly. But at this stage the vascular system is essentially that of a fish. A **ventral aorta** extends forwards from the heart, and from this structure four pairs of **afferent branchial** vessels extend into the third to the sixth visceral arches, supplying them with blood for oxygenation at the gills. Four pairs of **efferent** vessels carry this blood to the **lateral dorsal aortæ** for distribution. In the first two visceral arches rudimentary aortic arches appear.

Veins are formed in a similar manner. A pair of **vitelline** veins returns blood to the heart from the liver and yolk cells, whilst on either side of the dorsal aorta lies a **posterior cardinal** vein. Each extends forwards to form the **anterior cardinal** vein. Now both the anterior and the posterior cardinal veins lie in the body-wall, and are thus separated from the heart by the cœlom. But in the region of the heart the somatopleur sends a shelf inwards and the splanchnopleur outwards. These meet and fuse to form the transverse septum, cutting off the pericardium from the remainder of the peritoneal cavity. It is across this transverse septum that a **ductus Cuvieri** is developed on either side to establish communication between the heart and the cardinal veins. These ductus Cuvieri eventually become the **anterior venæ cavæ,** whilst a posterior vena cava is developed in the dorsal mesentery. Finally each of the vitelline veins becomes subdivided into an anterior and posterior region. The former connects the liver with the heart and is known as the **hepatic** vein, whilst the posterior region conveys blood from the gut to the liver, and thus forms the **hepatic portal** vein. Each posterior cardinal vein later becomes interrupted on its journey back to the heart, for it penetrates the kidney of its own side and thus the portion of it posterior to this organ is the **renal portal** vein.

During the process of metamorphosis, later to be described in greater detail, important changes occur with regard to the arteries in particular, for these must be so modified as to accommodate respiration by lungs instead of by gills. The blood-supply to the gills becomes very much reduced by the establishment of connexions between the afferent and efferent branchial vessels, whilst from the vessel of the sixth arch on either side a branch passes to the rudimentary lungs, so that in this way a **pulmonary** artery is formed. The vessels of the fifth arch now disappear, whilst those of the fourth become the **systemics** and those of the third the **carotids.** The vessels of the first two arches never develop beyond mere rudiments, and even these now disappear completely. Finally all dorsal connexion between the pulmonary, systemic and carotid arches, previously effected by the lateral dorsal aortæ, is lost, so that the arterial system is now practically of adult form.

External Features. In conclusion the changes which are visible externally during the development of the frog will be considered. These are sharply divisible into those of the earlier development, up to the fully formed tadpole stage, and those which accompany metamorphosis.

(A) Development of Tadpole. At first the egg is spherical, but soon becomes elongated, a distinct head-region becoming visible as a result of a slight constriction. After about two weeks this embryo escapes from the jelly in which it is embedded, and soon there may be distinguished rudimentary eyes and nostrils, and a groove denoting the future position of the mouth appears. Behind this groove is a rounded, ventral, **cement gland,** by means of which the newly-hatched tadpoles attach themselves in clusters to water-weeds. The object of this is to obtain a plentiful supply of oxygen, for by the process of photosynthesis the green plants are continuously liberating this gas in sunlight. On either side of the head two blunt projections appear, followed by a third. These become much branched and form the external gills. If a tadpole be examined under the microscope at this stage blood may be seen circulating in the filaments of the external gills. Together with the skin these gills effect respiration, for the surface of the body is ciliated and thus the water surrounding it is being continuously renewed. Up to this stage food takes the form of the yolk of the original egg, lying now in the floor of the posterior end of the gut. About a week after hatching a mouth appears, bordered

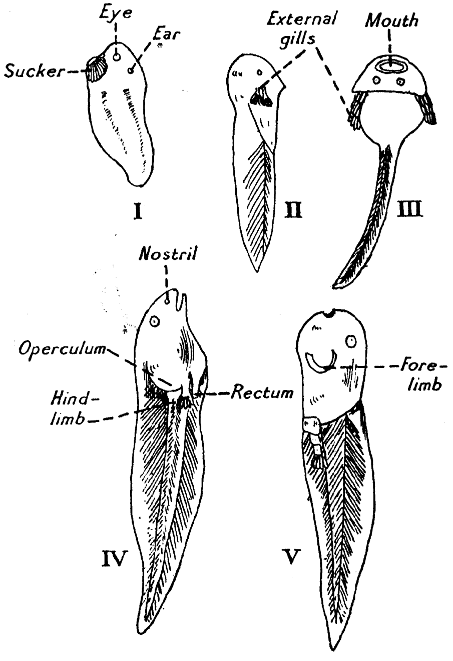


FIG. 160.—*Rana.* Successive stages in development of tadpole larva.

by a pair of horny jaws. The tadpole now feeds on minute plant organisms, and the gut may be seen by transparency through the body-wall as a coiled tube. At this time the gill-slits become perforated, four pairs in all, and on their walls they develop lamellæ, which become highly vascularised. A fold of skin now appears on either side, just in front of the most anterior gill-slit. These two folds extend backwards and become fused behind the last gill-slit with the body-wall, except for a small **opercular spout** to the left of the midventral line. Thus the gill-slits become completely enclosed within the **opercula.** The external gills now gradually disappear, and the hind-legs are first discernible as small swellings, which later become regionally differentiated into the various parts of the limbs. Fore-limbs are also formed now, but at first they are obscured by the opercula. By about the twelfth week the left one has come to protrude through the opercular spout, whilst the right one bursts through the operculum of its own side. At this time the tadpole may become in part carnivorous, whilst respiration, at first purely fish-like, may later become more adapted to life on land, for the tadpole may be seen frequently to rise to the surface and gulp in air, which enters the rudimentary lungs. This fully-formed tadpole is known as a **larva**, for it is a stage in the life-history of the frog, dissimilar in structure from the adult, but leading an independent existence. An embryo, on the other hand, is merely a stage in development, but is incapable of living independently. Larva-formation is almost always followed by something akin to metamorphosis—the series of rapid changes resulting in the assumption of adult form by the organism. A number of clearly-defined changes occurs in the tadpole.

(B) METAMORPHOSIS. Thus the skin is cast after feeding has ceased. The horny jaws are shed, and the gape of the mouth widens. In consequence of the change from herbivorous to carnivorous habits the gut shortens, for the food taken more closely resembles in chemical nature the tissue of the animal's own body and thus needs be changed less severely in the process of digestion. The gills eventually atrophy completely, whilst the tail is absorbed by the phagocytes of the blood. It is largely through this that the animal is nourished during this period of restraint from feeding. It is not until the third year of its life that the frog becomes sexually mature.

CHAPTER XIX

EMBRYOLOGY OF GALLUS

Fertilisation. The "yolk" of an hen's egg is in reality one cell, largely composed of reserve food material and, at one end, a small disc of living matter. This latter marks the position of the animal pole of the egg, to which attachment was effected whilst contained within the ovary. The egg is immediately surrounded by a delicate **vitelline membrane,** whilst the yolk itself is arranged in layers. When the egg is liberated from the ovary (only the left ovary persists in birds) it passes into an oviduct, along which it moves in such a way that its axis of symmetry is at right angles to the length of this tube. At copulation sperms are inserted by the cock into the base of the genital tract of the female, from which region they swim to the upper end of the oviduct, where fertilisation occurs. During the passage of the fertilised egg to the exterior albumen, inner and outer shell-membranes and the shell itself are secreted by the wall of the oviduct and plastered on to the yolk. Between the two shell-membranes there occurs at the blunt end of the egg a small air space. Owing to an axial rotation by the egg at this time the thickened threads, or **chalazæ,** by which the egg is suspended in the albumen, become spirally coiled. The shell itself consists of horny matter, impregnated with the phosphates and carbonates of magnesium and calcium. Superficially there is laid down a variable amount of pigment. Thus the egg is self-contained, and from the outside demands only a certain limited temperature in order that development may ensue. Unlike the frog and *Amphioxus,* there is a limited supply even of water available, so that water-metabolism must needs be carefully regulated. Since the shell and membranes are permeable there is an adequate supply of oxygen available.

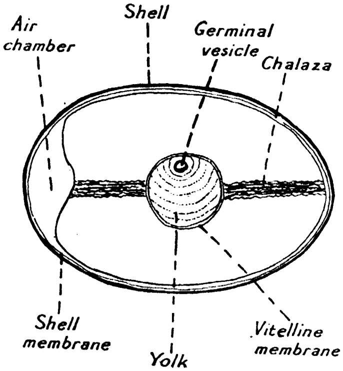


FIG. 161.—*Gallus.* Egg in longitudinal section.

Cleavage. So great is the quantity of yolk in the egg of *Gallus* that cleavage is only partial, or **meroblastic.** That is to say that the whole egg does not take part in it, or that cytoplasmic cleavage does not keep pace with nuclear division. The first cleavage furrow appears at about the time when the albumen is being added to the egg, whilst by the time the shell has been formed it is at the eight-cell stage. When the egg is laid the blastula stage has been passed, and a certain amount of gastrulation has already occurred. Thus considerable difficulty in obtaining the early stages of development is experienced.

The amount of cytoplasm is very small, and cleavage results in the formation first of a flat disc of cells, known as the **blastoderm.** Around the entire margin this merges into the yolk, from which it is separated beneath by a small cavity. This is the **blastocœl.** The circular zone where the blastoderm is continuous with the yolk is known as the **periblast,** which, owing to its comparative opacity, is termed the **area opaca,** in contrast to the clearer blastoderm within, called the **area pellucida.** The blastoderm later extends further over the yolk, so that the area opaca is increased in dimensions. This is in no way comparable to the spreading of the cells of the animal pole over those of the vegetable pole in the frog, nor, indeed, has it any morphogenetic significance.

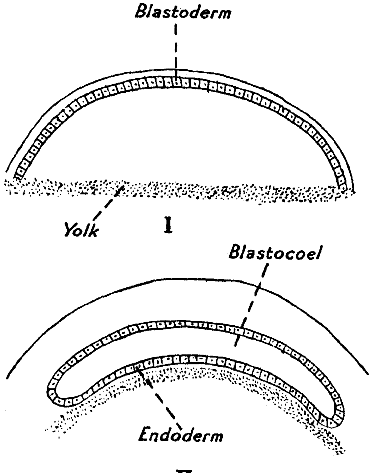


FIG. 162.—*Gallus.* Blastoderm, showing formation of endoderm.

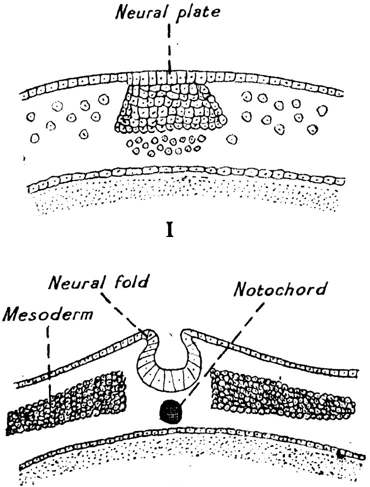


FIG. 163.—*Gallus.* Formation of nerve-cord, notochord and mesoderm.

Gastrulation. **Endoderm** is formed by delamination from the under surface of the blastoderm. This endoderm extends outwards beneath the upper layer of the blastoderm, and merges into the periblast. It is at about this stage that the egg is laid, some twenty-four hours having elapsed since fertilisation.

In the middle of the area pellucida there is now developed in the upper layer of the blastoderm a thickening, known as the **primitive streak.** This lies at right-angles to the length of the egg and is formed from in front backwards. Along this primitive streak appears a shallow **primitive groove,** ending anteriorly in the form of a blind **primitive pit.** This is bordered on its anterior margin by a raised **primitive knot.** This primitive knot represents the dorsal lip of the blastopore of lower forms, whilst the walls of the primitive groove represent the lateral lips of the same structure.

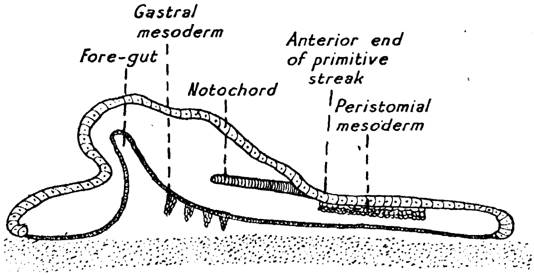


FIG. 164.—*Gallus*. Longitudinal section. Notochord and mesoderm formation.

All that remains of the aperture of the blastopore is the primitive pit and the primitive groove. As this primitive streak extends backwards it behaves as does the lip of the blastopore of lower forms, leaving behind it a trail of **mesoderm** cells on either side and, down the middle line, a rudimentary notochord, which is formed principally from cells proliferated from the primitive knot. The mesoderm is therefore described as peristomial. But at the extreme front end of the animal (i.e. the part anterior to the position of the future fore-brain) the mesoderm and the forward extension of the notochord are produced by delamination from the endoderm, so that this mesoderm is described as gastral. Thus the gastrula stage is arrived at without the process of invagination. After the formation of the notochord and mesoderm the upper layer of the blastoderm becomes known as the **ectoderm.**

Formation of Head-fold. From this point onwards the development of the chick embryo differs considerably from that of lower forms, for there are now formed embryonic membranes, within which the developing organism becomes almost completely enclosed.

No doubt this is in adaptation to development on land, for the embryo becomes suspended in a liquid medium, principally water, and this serves as a substitute for the water in which the embryos of lower forms develop. The first sign of the formation of these membranes is the raising of an **head-fold.** This takes the form of a forward evagination of the ectoderm, mesoderm and endoderm from beneath the anterior end of the embryo, and in this way a floor is formed to the region of the future fore-gut. Meanwhile the mesoderm has become segmented and a split occurs in it, representing a rudimentary cœlom, the inner wall of which gives rise to the **myomeres** in the region of the notochord, whilst below the inner wall represents the **splanchnopleur** and the outer wall the **somatopleur.** The ectoderm, mesoderm and endoderm all become extended outwards in all directions beyond the limits of the embryo, so that this region of extraneous growth is described as extra-embryonic, and into its mesoderm extends the cœlomic cavity. As this process occurs blood-islands are developed in the mesoderm, so that the growth may be observed as that of the gradual creeping of an **area vasculosa** over the original area pellucida. Two horns of these extra-embryonic tissues extend forwards and eventually meet in front to enclose a small, clear region, known as the **proamnion,** immediately in front of the head-fold.

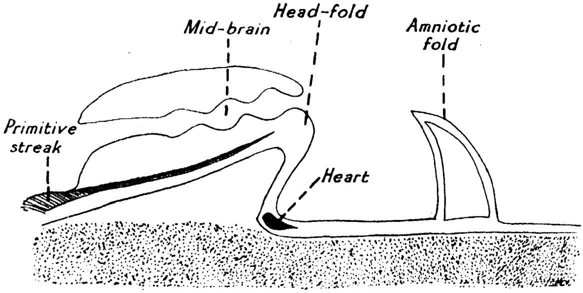


FIG. 165.—*Gallus.* Formation of amnion and head-fold.

Nerve-cord. During this process the **neural plate** is formed as a thickened plate of ectoderm cells along the axis of the embryo, appearing progressively from in front backwards as the primitive knot recedes towards the hind end of the embryo. On either side of the middle line a neural fold arises, and these two folds eventually fuse in the mid-dorsal line to form an hollow nerve-cord. The extreme lateral portion of each fold gives rise to a **neural crest,** as in the frog.

Formation of the Amnion. The amnion is one of the embryonic membranes referred to above as serving to enclose the organism during its subsequent development. As well as assisting in the regulation of water-metabolism the liquid it contains acts as a buffer to absorb mechanical shocks, and also to minimise changes of temperature. It is developed from extra-embryonic ectoderm and mesoderm, and arises first as an evagination of these layers immediately in front of the proamnion. This grows backwards over the embryo, and lateral folds also arise in a similar manner, extending right to the posterior end, so that eventually the whole embryo is enclosed dorsally by a sac formed of two layers of extra-embryonic ectoderm, the inner of which is known as the **amnion** and the outer as the **chorion.** These layers are lined each with extra-embryonic mesoderm, and between the two layers of mesoderm is extra-embryonic cœlom. The amnion and chorion remain in contact only at the extreme hind end, forming the **sero-amniotic connexion.** By the inward extension beneath of these amniotic folds a ventral surface is formed to the gut of the embryo through the effecting of a folding process so that the dorsal surface of the embryo becomes raised from the blastoderm. This occurs first at the anterior and posterior ends, so that in these regions a floor is formed to the gut, whilst the middle portion still has no floor. The passages between the floorless region and the two floored parts of the gut are known respectively as the anterior and posterior **intestinal portals,** which approach each other progressively more closely as further floor is formed to the gut. Finally this region of open communication between the yolk and embryo is confined to a very small area, known as the **umbilicus.** The yolk itself has become almost completely enclosed in a **yolk-sac,** formed by the extension all round of the blastoderm. This extra-embryonic tissue consists

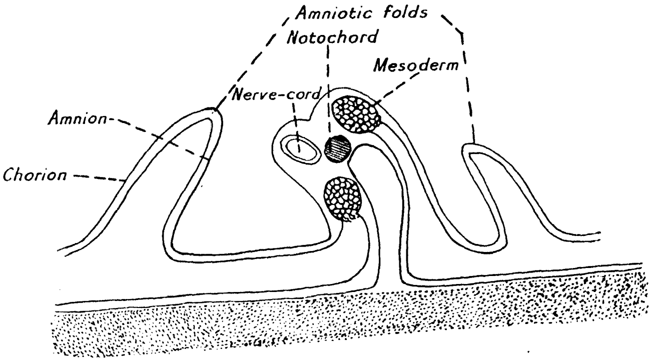


FIG. 166.—*Gallus.* Transverse section to show formation of amnion.

of an outer layer of ectoderm, really a ventral continuation of the chorion, whilst the yolk is immediately covered by endoderm. Between the endoderm and the ectoderm lies extra-embryonic mesoderm, enclosing the extra-embryonic cœlomic cavity.

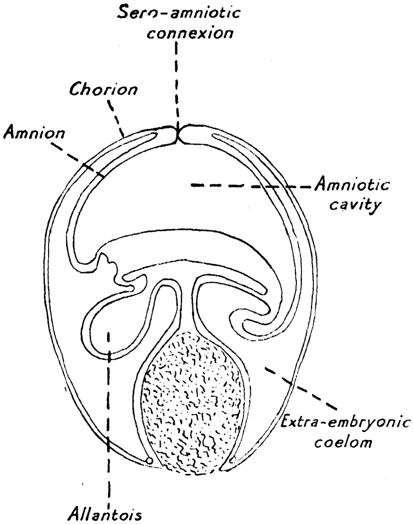


FIG. 167.—*Gallus*. Longitudinal section to show amniotic cavity and allantois.

Allantois. A second embryonic membrane starts to develop soon after the formation of the amnion. A median evagination from the floor of the hind gut is the first signs of this membrane, or allantois. It increases greatly in size and grows out ventrally into the extra-embryonic cœlom. Meanwhile the yolk-sac has become closed, so that the yolk is completely contained within it. As the allantois grows so the yolk-sac diminishes in size. Soon it comes to enclose almost the whole embryo, its outer layer being separated from the chorion and its inner from the amnion merely by a double layer of mesoderm, which itself later undergoes fusion with each layer of the allantois to form a single membrane. Thus, but for this compressed layer of mesoderm, the outer layer of the allantois is now applied to the chorion, which itself lies in close

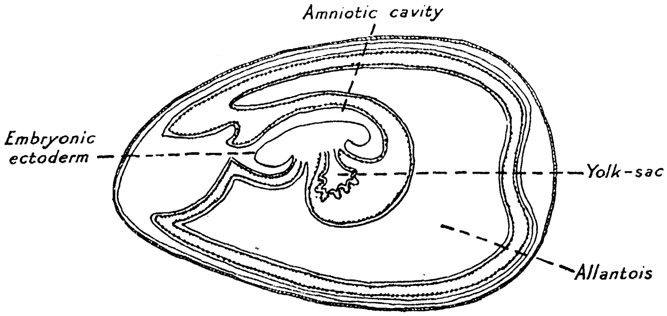


FIG. 168.—*Gallus*. Longitudinal section to show embryonic membranes. (Mesoderm shown in dotted line.)

contact with the porous shell, from which it is separated only by the shell-membranes. Thus the allantois becomes the respiratory organ of the embryo, for it is highly vascularised. But the allantois acts also as an organ of excretion, for the Wolffian ducts, formed as in the frog, run into the cloaca near the origin of the allantois. The waste products accumulated during development are stored in the allantois which, in fact, is homologous with the urinary bladder of *Rana*.

Vascular System. This is well established by the third day. Blood is collected up from the area vasculosa into a pair of **anterior vitelline** veins. These unite to form a median **ductus venosus** just in front of the anterior intestinal portal. This vessel corresponds to the subintestinal vessel of the frog, and like it becomes differentiated to form an heart. **Aortic arches** are formed, and altogether four pairs of gill-slits are developed, the first (most anterior) three of which become perforated to communicate with the amniotic cavity. The vessels in the visceral arches between these slits communicate on each side with a **lateral dorsal aorta,** which latter structures fuse posteriorly to form a median vessel. This fish-like arrangement does not last long, for the vessel in the fourth visceral arch disappears on the left side, whilst that of the right side becomes the systemic. The pair of vessels in the sixth arch give rise to the **pulmonary** arteries in connexion with the systemic by the **ductus arteriosus.**

Anterior and **posterior cardinal veins** are developed in the body-wall as in the frog, and these reach the heart by the formation of a pair of **ductus Cuvieri** running in the transverse septa, also arising as in *Rana*.

The supply to the allantois is of importance, since this organ functions for both respiration and excretion. At first blood from this organ is returned by a pair of **umbilical** veins to the ductus Cuvieri of each side. Later the right one degenerates and the left one opens directly into the ductus venosus. When septa have been laid down to divide the heart into right and left auricles and ventricles this blood comes to run into the right auricle, whilst the pulmonary veins are developed connecting the lungs with the left auricle. But at this stage the lungs are not functional, so the septum between the auricles breaks down to permit the passage of oxygenated blood direct to the left side of the heart. Blood which leaves the right ventricle would normally go to the lungs, but this is avoided by means of the ductus arteriosus, so that for the time being all blood leaving the heart reaches the systemic arch. Only at hatching is the interauricular septum again completed.

Kidneys. The pronephros and mesonephros develop as in the frog, but they are later replaced by the adult kidney, the **metanephros.** This is formed posterior to the mesonephros from the nephrotomes of that region, known collectively as the **metanephrogenous tissue.** The ureter, by which urine is passed to the cloaca from each metanephros, arises as a lateral diverticulum from the base of the Wolffian duct. This grows forwards and branches to form collecting tubules, which penetrate the metanephros. The kidney itself is richly vascularised, and Bowman's capsules, each containing a glomerulus, are formed as in the frog.

The original Wolffian duct is conserved in the male as a vas deferens for the conveyance of sperm to the cloaca. A Müllerian duct is developed in both sexes from cœlomic epithelium, a plate of this tissue becoming closed over to form a tube after the manner in which the nerve-cord is developed. Both these ducts later disappear in the male, whilst in the female the left one alone remains as the oviduct, since there is no right ovary in birds.

The development of feathers is described in Chapter XXIV.

CHAPTER XX

THE ALIMENTARY SYSTEM

IN this and succeeding chapters the actual structure of the various systems in the Chordata will be treated comparatively, whilst considerations of their physiology will be reserved until later, when the bodily functions of invertebrates will be included in the comparisons.

The alimentary system is composed in all the Chordata of a closed tube, the alimentary canal, leading from mouth to anus, together with a number of diverticula arising from it. The extreme anterior and posterior ends of the alimentary canal are lined by ectoderm, and are known respectively as the **stomodæum** and **proctodæum.** They originate as invaginations of ectoderm, and this becomes continuous with the endoderm constituting by far the greater part of the gut.

The alimentary canal itself is primitively a straight tube, but in higher forms it becomes longer than the body and differentiated into a number of distinct regions. Thus in *Amphioxus* there is present a simple, straight tube, undifferentiated of itself, but with the region bearing the gill-slits distinguished from the remainder by the term pharynx. In all the Gnathostomata the gut has become bent or coiled so that its increased length may be accommodated within the body-cavity. This process occurs similarly in all five classes, though progressively to a greater extent as evolutionary development is traced upwards from the fish. Thus the stomach becomes a sacculated organ opening from the œsophagus, and from its distal (pyloric) end the gut kinks to the right. In this way the duodenum is formed. It is the region beyond the duodenum which becomes so greatly extended in forms above the fish. In the latter group this consists of an almost straight intestine, connected by a narrow rectum with a cloaca. In Amphibia the intestine becomes considerably coiled, thus aiding in the process of absorption through the increase of internal surface. In the dogfish this same result is obtained by the presence of the spiral valve. In reptiles the position is much the same as in the frog, but in birds the rectum is peculiar on account of its incomplete transverse division into three regions. Innermost of these is the **coprodæum,** followed by the **urodæum,** into which open the ureters and genital ducts, and this is connected with the cloacal aperture by the proctodæum. In mammals the intestine may be subdivided into a small and large region. The small intestine consists of a very long, much coiled, narrow tube, terminating in a swollen sacculus rotundus. From this the large intestine, in the form of a wide colon and rectum, leads to the anus, which aperture has become separated from the common cloaca found in lower forms. At the origin of the large intestine there is given off a blind diverticulum, the cæcum, ending in a vermiform appendix.

The stomach itself is not without certain modification in some groups. Thus in birds it consists of two regions, namely, an anterior, thin-walled proventriculus, and a posterior, horny gizzard, where mastication occurs. In mammals the stomach lies transversely just below the diaphragm. It is curiously modified in the group known as the Ruminants, which mammals are characterised by the chewing of their "cud." Accordingly there is an anterior region to the stomach, consisting of the **paunch** and **reticulum,** into which the food is passed during the process of eating. When this ceases the food is regurgitated from this chamber and masticated in the mouth. On swallowing the salivated food passes through the chambers in which it had previously been trapped into the remaining chambers of the stomach, known as the **maniplies** and **abomasum.** Here gastric juice is formed. The phenomenon is in adaptation to the habits of the ruminants, for they are exclusively herbivorous and, in the wild state, are preyed upon by carnivorous forms. Thus when they come out on to the open grassland for their food it is an advantage for them to take it quickly, and afterwards return to shelter to masticate it.

The œsophagus in birds becomes enlarged to form a crop, where food is temporarily stored.

In *Amphioxus* and fish the anterior part of the gut, known as the pharynx, is modified by the perforation of gill-slits, establishing communication between the lumen of the gut and the exterior. These are formed during development of the members of the higher groups, but in mammals they remain closed. Only one pair of them persists, however, taking the form of the Eustachian tubes.

In the forms constituting the Cephalochordata, exemplified by *Amphioxus*, the mode of feeding is ciliary, and the gut is modified in a manner already described. But in the Gnathostomata themselves the most anterior visceral arches are modified to form the jaws. Accordingly much larger food can be manipulated, and only occasional patches of cilia occur on the epithelium lining the gut. Food is now propelled along the gut by peristalsis instead of by the beating of cilia. The endostyle of *Amphioxus*, so important in relation to the ciliary mode of feeding, becomes completely closed off in the Gnathostomata to form the thyroid gland beneath the floor of the mouth. In the margin of the jaws teeth are present, the development and structure of which are described in Chapter XXIV.

As well as the actual canal itself there is a number of diverticula to be considered in relation to the alimentary system. The first definite digestive gland to make its appearance is the liver diverticulum of *Amphioxus*. In the Gnathostomata this becomes a large, lobed organ, connected with the duodenum by a bile-duct, which, except in birds, originates as a swollen gall-bladder. A pancreas is formed similarly in all Gnathostomata, communicating with the duodenum either by the bile-duct, as in *Rana*, or by a duct of its own, as in *Lepus*. Salivary glands appear first in some Amphibia, though they are not present in *Rana*. Their absence in the fish is explicable on the grounds of the current of water which is being passed continually through the mouth to escape *viâ* the gill-slits.

In all forms above the fish a median, ventral outgrowth from the pharyngeal region gives rise to a pair of lungs, whilst at the posterior end of the gut a similar evagination forms the urinary bladder.

CHAPTER XXI

VASCULAR AND RESPIRATORY SYSTEMS

VASCULAR SYSTEM

THE object of the present chapter is to display the fundamental similarity between the blood systems of the various groups of Chordata already studied by means of selected types.

The general plan of the chordate vascular system is almost precisely that displayed by *Amphioxus*. Thus it consists essentially of four vessels. Lying in the ventral part of the body-wall is the subintestinal vessel, passing forwards. This sends paired branches up the visceral arches to communicate with the lateral dorsal aortæ in the body-wall. Posteriorly these two vessels unite to form a median dorsal aorta, from which blood is supplied by segmental vessels to the body-wall, and by vessels in the mesentery to the gut. Blood from the gut-wall is collected up direct into the subintestinal vein, which vessel is interrupted during its passage forwards by the liver diverticulum, in which it breaks up into capillaries to deposit much of its stored carbohydrate material before continuing its journey. Deoxygenated blood from the body-wall is received by a pair of cardinal veins, which are in connexion with the anterior end of the subintestinal vessel by a pair of ductus Cuvieri, running in the transverse septa across the cœlomic cavity. Primitively there was no specialised heart, for the majority of the vessels were contractile. Keeping this state of affairs in mind it is possible to trace he development of the heart and main blood-vessels of the various classes of Gnathostomata up to the most highly developed condition found in mammals and birds.

Heart. In the fish the anterior end of the subintestinal vessel has become modified to form a pumping organ, as a result of which the general contractibility of the remaining vessels has been lost. The veins (called sinuses on account of their large size) open into a sinus venosus, which communicates with a thin-walled auricle. From thence blood is passed into a thick-walled ventricle, produced forwards to form a contractile conus. Running forwards from this is that portion of the subintestinal vessel known as the ventral aorta, from which the aortic arches arise. The base of the ventral aorta is swollen to form a bulbus arteriosus, distinguishable from the conus in that, whereas the wall of the latter is of cardiac muscle, that of the bulbus is of the ordinary involuntary variety.

In the Amphibia, represented by the frog, the auricle has become divided into right and left halves, the former receiving the deoxygenated blood from the sinus venosus and the latter oxygenated blood from the lungs. The main artery, the truncus arteriosus, is divided transversely by a row of three semilunar valves into a proximal conus and a distal bulbus, while it is partially divided longitudinally by a spiral valve.

But it is in the Reptilia that the most important differentiation has occurred in respect of the structure of the heart, for such has taken two independent courses. In the group known as the Therapsida the truncus is split into two right down to the base. One of these forms the pulmonary canal, supplying the lungs and opening from the right side of the heart. The other is the systemic arch, only the one on the right side persisting, and this opens from the left ventricle. The heart itself has become completely divided into right and left auricles and ventricles, and this line of evolutionary development culminates in the mammals, where there is no sinus venosus, but the three great veins open independently into the right auricle, whilst the conjoined pulmonary veins open into the left auricle.

The other group of Reptilia, known as the Sauropsida, has become differently specialised in respect of the structure of the heart, and their development leads up to the condition found in birds. The truncus has this time become split to its base into three channels, two of which constitute the systemics (right and left), and the third the pulmonary. The two systemic arches cross, so that the right one arises from the left ventricle and the left one originates in common with the pulmonary arch from the right ventricle. In most reptiles the septum between the right and left ventricles is incomplete, but in birds there is no communication between the two ventricles. It will be observed, therefore, that the left systemic arch can distribute only deoxygenated blood, since it arises with the pulmonary arch from the right ventricle. Accordingly it disappears in birds, where the single, persistent systemic arch is the right one, in contrast to the left of mammals. As in mammals there is no sinus venosus in birds, whilst in both groups deoxygenated blood is returned to the right auricle and oxygenated to the left.

Arteries. In the primitive condition the arteries arise in the form of paired aortic arches from the ventral aorta and pass up the walls separating the visceral pouches. These are the afferent branchial arteries. On reaching the gills they break up into capillaries, and there the blood becomes oxygenated. This blood is then collected up into a corresponding number of paired efferent branchial arteries and conveyed to a pair of lateral dorsal aortæ. These pass backwards and unite to form the dorsal aorta, distributing blood to all parts of the body behind the pharynx, whilst they are also extended forwards to supply the head. Thus the blood is not returned to the heart after oxygenation, prior to distribution to the tissues. Instead it is carried round the body direct from the gills. Thus only deoxygenated blood reaches the heart, which is consequently described as " venous." This primitive condition obtains in *Amphioxus* and fish.

In the Amphibia the fish-like circulation is perfectly developed in the larval stages, such as the tadpole of the frog. This is manifestly in adaptation to an aquatic mode of life, but during metamorphosis the arterial system assumes the form suitable to terrestrial existence. Thus it is the supply to and from the gill-slits which must needs be modified, whilst blood must now be distributed to the lungs for oxygenation. The afferent and efferent vessels become directly connected, so that the gills are now circumvented. The aortic arches of the first two visceral arches disappear, though they are never more than rudimentary. The vessels of the third arches become the carotid arches, being continued forwards to the head as the lateral dorsal aorta of each side. In the frog the vessels of the fourth visceral arch form on either side a systemic arch. These unite with the posterior portions of the lateral dorsal aortæ, which two structures join to form a median dorsal aorta. The aortic arches of the fifth visceral arches disappear in *Rana*, though in some Amphibia these, like those of the fourth, form a pair of systemic arches. The arches of the sixth visceral arch become the pulmonary arches, one passing to either lung. The carotid, systemic and pulmonary arches on either side almost always become completely closed off from each other distally, this entailing the loss of intermediate portions of the lateral dorsal aortæ. Where such connexions remain that between the carotid and the system arch is known as the **ductus caroticus,** and that between the systemic and pulmonary as the **ductus arteriosus.**

In birds and mammals the aortic arches of the first, second and fifth visceral arches disappear, whilst those of the third, fourth and sixth become modified as in the frog to form the carotid, systemic and pulmonary arches respectively. As has already been pointed out, the truncus in birds is divided to its base into three channels, the right and left systemics and the pulmonary. The left systemic arch disappears, whilst the two pulmonary arches lead into the pulmonary channel, which itself opens from the right ventricle.

In mammals the systemic arch persists complete only on the left side, whilst the right systemic is represented by the very short innominate artery, communicating with the carotid and subclavian of its own side. The left systemic becomes known as the aorta, and from it open the carotid and the subclavian arteries of that side. The lateral dorsal aorta is preserved on either side in the form of the internal carotid artery to the brain, whilst the anterior extension of the ventral aorta becomes the external carotids. These arrangements are made clear in the accompanying figure.

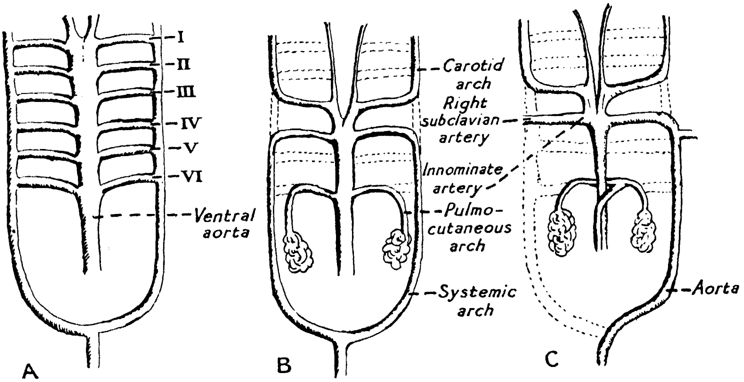


FIG. 169.—Diagrams of arterial arches in A. Dogfish. B. Frog. C. Mammal.

Modifications such as those described above are developed in relation to a terrestrial mode of life, as well as to a complete separation of the heart into right and left sides, so that oxygenated and deoxygenated blood may be kept apart.

Veins. All deoxygenated blood is collected up by a number of vessels and returned eventually to the heart. Primitively these consist of a subintestinal vessel to receive blood from the gut, and a pair of cardinal veins draining the body-wall and being in connexion with the anterior end of the subintestinal vessel by a pair of ductus Cuvieri. The subintestinal vein becomes interrupted by the liver diverticulum, so that the portion of this vein on the side of the liver away from the heart is the hepatic portal vein, whilst the hepatic vein carries blood from the liver into the heart. This is typically the condition in *Amphioxus*. In the fish the arrangement is very similar, whilst two pairs of vessels—the subclavian and pelvic—are developed for the return of the blood from the anterior and posterior limbs respectively. Furthermore, with the development of mesodermal kidneys, the posterior cardinal veins become interrupted and break up into capillaries in these organs. The portion of each posterior cardinal vein behind the kidney now becomes known as a renal portal vein. An hepatic portal vein returns blood from the gut to the liver, and corresponds to the structure of the same name in *Amphioxus*. Deep in the body-wall a pair of lateral veins is developed.

In the Amphibia certain further changes have taken place. Thus the anterior portion of the posterior cardinal vein has disappeared, whilst a new structure, the posterior vena cava, has been developed to replace it. The only portion of the posterior cardinal veins to persist is the renal portal vein on each side. The lateral veins of the fish have become coalesced in the midventral line in the frog to form the anterior abdominal vein, which now no longer reaches a ductus Cuvieri or the sinus venosus, but leaves the body-wall to penetrate the liver, thus contributing to the formation of the hepatic portal system, the remainder of which is constituted by the hepatic portal vein, homologous with that of the fish. The veins from the hind legs are also in communication with the renal portal vein.

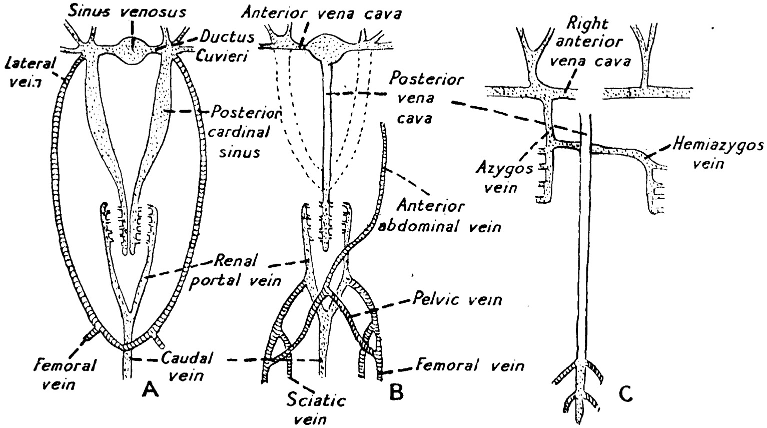


FIG. 170.—Diagrams of venous system of A. Dogfish. B. Amphibia. C. Mammal.

In mammals the anterior portion of the venous system still remains comparatively unchanged. Posteriorly, however, there is considerable specialisation. Thus the anterior abdominal vein disappears, whilst with the development of the metanephric kidney the renal portal system has been lost. The veins from the hind-limbs open direct into the vena cava, the posterior part of which is formed by the fusion of the hind ends of the posterior cardinal veins, whilst the anterior part is homologous with the structure of the same name appearing first in Amphibia. The anterior part of the posterior cardinal vein is represented on the right side by the azygos vein, returning blood from the body-wall in the region of the ribs, and by a short hemiazygos vein on the left side. This latter vein does not reach the ductus Cuvieri of its own side, but joins the azygos vein. The two ductus Cuvieri become known as the anterior venæ cavæ.

Lymphatic System. In conclusion the significance of this system in various classes of the Gnathostomata may be briefly described. It will be remembered that lymph is the fluid escaping from the blood to bathe the various tissues, and which is afterwards collected up into lymph-vessels, several of which may unite to form a lymph-sac. The lymph-vessels passing up the villi of the intestinal wall are called lacteals, whilst contractile lymph-sacs are known as lymph-hearts. The walls of lymph-vessels occasionally become secretory, and thus lymph-glands are formed. Examples of these are the spleen, tonsils and Peyer's patches in the mammalian intestine. In the fish the spleen is developed, whilst in Amphibia the skin is separated from the body-wall by lymph-spaces. All lymph-vessels eventually communicate with one of the great veins, though there are no lymph-hearts present in mammals.

RESPIRATORY SYSTEM

One of the chief functions of the blood is the distribution of oxygen. Accordingly it is found that the development of the vascular and respiratory systems is closely associated.

The primitive organs of respiration in the Chordata are gills. Gill-slits become perforated to communicate between the pharynx and the exterior. The walls of these slits become highly vascularised, and filamentous lamellæ extend into their cavities. Water is taken in through the mouth and passed out over these lamellæ, giving up oxygen to the blood and carrying away waste carbon dioxide as it does so. This condition obtains in a very primitive form in *Amphioxus*, though the gill-slits do not open direct to the exterior, but into a closed atrial cavity.

In the fish this simple arrangement becomes variously modified. Thus there are typically six pairs of visceral clefts, the first pair being smaller and more dorsal than the remainder and known as the spiracles. In the Chondrichthyes, to which the dogfish belongs, the slits open direct to the exterior, but in the Osteichthyes (bony fish) they are covered on either side by a flap of skin, known as an operculum. Water escapes from beneath the operculum in a stream from its posterior end, and actually assists in propelling the animal. Respiration is effected by the closing of the gill-slits and the lowering of the floor of the mouth, into the cavity of which water passes in consequence. The mouth is then closed and the gill-slits are opened. When the floor of the mouth is raised water is passed out through the clefts. In a few flat-fish the spiracle may be used to admit water to the pharynx, whilst in almost all bony fish this gill-slit is never actually perforated.

In some fish, however, lungs are developed. Most notably is this so with the Dipnoi, as mentioned on page 130. There are only three species living. In Protopterus and Lepidosiren there is a pair of lungs, whilst in Ceratodus these are represented by a single, median, ventral diverticulum. In these and certain other fish the lungs are actually used as organs of respiration, the sixth pair of branchial arteries becoming modified to form pulmonary arteries, whilst a pair of pulmonary veins returns oxygenated blood to the heart. It has been suggested that these lungs, and, indeed, those of higher forms, are modified gill-slits which do not communicate with the exterior on the surface of the animal.

In other bony fish the lung remains single and becomes highly specialised to form an air-bladder. This normally loses its connexion with the gut to become a closed sac, but it is still vascularised, though often by the cœliac artery, instead of by the last pair of visceral arches. In this condition it is used as an hydrostatic organ. Thus when its possessor moves to a greater depth in the water a certain amount of air is lost from the bladder by being absorbed into the blood of its vascularised wall, for the greater depth causes the air in the bladder to become compressed. Thus the specific gravity of the fish is increased and the new depth can be maintained without effort. When the fish moves nearer to the surface of the water the reverse process occurs.

In adult Amphibia respiration is effected very largely by a pair of thin-walled lungs. But in the larva gill-slits are present, employed as in the fish. Previous to their formation there appear on the surface tufts of external gills, acting as temporary respiratory organs. In the adult air is forced into the lungs under pressure, so that when the pressure is decreased air escapes to the exterior. It must be remembered that respiration is effected in Amphibia to no small extent through the vascularised skin.

In the remaining classes of the Gnathostomata air is drawn into the lungs as a result of the expansion of the thorax in which the lungs are contained. In mammals this process is further facilitated by the lowering of the diaphragm. A simple experiment may be made to demonstrate the principle on which this type of inspiration rests. A bell-jar is tightly fitted with a stopper, through which passes a short glass tube. To the end of this tube within the bell-jar is attached a thin-walled balloon, whilst the jar itself is half-filled with water. By means of a tap and delivery tube water is then allowed to escape from the bell-jar, when it is observed that the balloon expands owing to the reduction of air-pressure on its external surface.

Whereas the lungs of fish and Amphibia are thin-walled structures those of birds and mammals are spongy, being penetrated by innumerable air-tubes (alveoli) and capillaries, thus presenting a large surface for the purpose of gaseous exchange. Reptiles occupy an intermediate position, for, though their lungs are still essentially hollow sacs, the walls have become considerably folded within the cavity. In birds, moreover, diverticula from the lungs extend to various parts of the body, thereby rendering the body lighter, as well as which they make it possible for air to pass completely through the lungs into the air sacs at inspiration, so that, unlike other forms, it cannot remain in the blind ends of the alveoli. This is in adaptation to the enormous amount of kinetic energy required by the bird during flight, accounting also for the high body-temperature of birds (about 108° F.).

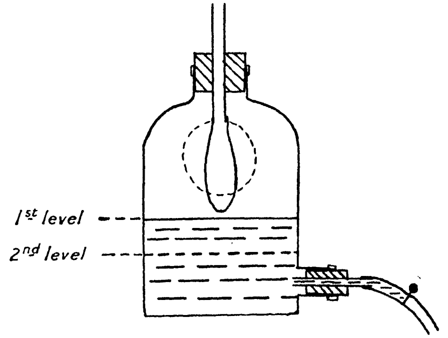


FIG. 171.—Experiment to demonstrate principle of mammalian respiration.

In mammals and some reptiles there is a further adaptation to terrestrial respiration in the development of the false palate, formed by a pair of shelves growing inwards from the maxillæ and completed behind by the palatines, so that a nasal passage is enclosed between this false palate and the true roof of the mouth. As already stated this false palate may be continued backwards in the form of a soft palate, and eventually the nasal passage opens by the secondary choana into the cavity of the mouth near the glottis. In further adaptation to breathing on land the glottis is closed during swallowing by a flap of skin, termed the epiglottis, whilst in some aquatic forms—e.g. the whale—the glottis may be inserted into the secondary choana, so that there is no possibility of water or food entering the trachea.

It is essential for embryos to effect respiration. This is brought about in various ways in different groups of Gnathostomata. Thus in the larvæ of fish and Amphibia gill-slits are developed, whilst when these are not formed sufficiently early they are preceded by external gills as outgrowths from the body-wall. The reptiles, birds and mammals are together known as the Amniota, for they are characterised by the formation of an amniotic cavity to accommodate development on land. In reptiles and birds the allantois is the respiratory organ, for it becomes closely applied to the permeable shell, so that gaseous exchange can take place, as already described on page 235.

Certain portions of the respiratory system have become modified in connexion with the production of sound. Thus in the male frog there is a pair of vocal sacs opening laterally into the pharynx, and these are used as resonators to facilitate the making of the characteristic croaking sounds. In birds and mammals vocal cords are formed as thin bands of connective tissue attached transversely within the larynx. These may be set in vibration and sounds thus produced. In birds this same development has taken a rather specialised form, and is known as a syrinx. Just where the trachea divides to form two bronchi the cartilages assume the form of only half rings, so that half the wall remains membranous. A membrane—the pessulus—projects from the junction of the bronchi some distance along the trachea, and thus the syrinx is formed. In this connexion it is interesting to note that the ability to produce sounds has been evolved to an extent comparable to the ability to receive them, as determined by the degree of development of the cochlear part of the ear.

In the Dipnoi and all the Tetrapoda (i.e. all classes of Gnathostomata except the fish) air (or water in the case of the Dipnoi at certain times) enters the cavity of the mouth by the nasal passages. It perhaps becomes expedient for this air to be tested as to its purity, and in consequence the epithelium lining the nasal chambers becomes highly sensitive. The olfactory organs thus lie in close association with the respiratory system.

To sum up, the purpose of the respiratory system is to expose as large a surface of blood as possible to the air, so that gaseous exchange may be effected. This is done by gills in aquatic forms and lungs in animals leading a terrestrial mode of life. Exceptions to this latter generalisation are known, for the Dipnoi possess lungs, which serve for respiration, whilst the whale, which has reassumed an aquatic mode of life, also breathes by lungs.

CHAPTER XXII

THE URINO-GENITAL SYSTEM

In the description of the dogfish, frog and rabbit the structures associated with the elimination of waste products and with the elaboration and evacuation of germ-cells were described individually. It now remains, therefore, to trace the relationship between them.

Origin and Development of the Kidney. The mesodermal pouches formed by evagination from the endoderm in the typical development of a Chordate prototype soon become extended ventrally to enclose the gut in a spacious cœlom, bordered by an inner and outer wall. Dorsally, in the region of the nerve-cord and notochord, segmentally-arranged pouches become separated from the ventral cœlom by the formation of transverse septa. Connecting each segmental dorsal pouch with the splanchnocœl beneath is a narrow intermediate cell-mass or nephrotome. It is at this stage that development of the kidney begins. The cavities of the most anterior nephrotomes, known as the nephrocœls, establish communication with the cœlom by means of cœlomic funnels, known as cœlomostomes, whilst a lateral evagination of the wall of each nephrotome grows towards the body-wall. Meanwhile a rod of mesoderm cells has become cut off from the outer wall of the splanchnocœl (i.e. from the somatopleur), and this becomes hollowed out to form a tube extending backwards as far as the cloaca, with which it communicates. The evaginations of the walls of the nephrotomes open into this tube, so that the cœlom is now in connexion with the exterior. The blind end of each branch becomes invaginated to form a Bowman's capsule. Into this passes a branch from the dorsal aorta and one from the cardinal vein, breaking up into capillaries within the capsule to form a glomerulus. The composite structure—capsule plus glomerulus—constitutes a Malpighian corpuscle. In this way the pronephros is formed, and this may be regarded as the functional kidney in the early embryo of our prototype.

Later another set of tubules arises from the nephrotomes immediately posterior to the pronephros. They find the pronephric duct already made for them, and they quickly establish communication with it. Branching occurs to form a mass of intercommunicating kidney tubules, each with its associated glomerulus. This constitutes the mesonephros, and the original pronephric duct becomes known as the Wolffian duct, the pronephros itself disappearing. The mesonephros thus replaces the pronephros as the functional kidney.

Finally a third kidney is developed posterior to the first two. In a manner similar to that already described kidney tubules are formed, but these do not communicate with the Wolffian duct. Instead a diverticulum arises from the base of the duct on either side, and grows forwards. This is the ureter. When it reaches the level of the new kidney it sends branches into it, and these eventually communicate with the kidney tubules, which by this time have become very much subdivided and vascularised. This structure is the metanephros, and it is the functional kidney of the adult.

Formation of Gonads and the Origin of their Ducts. The gonads arise similarly in both sexes, though they are quickly differentiated into potential ovaries or testes. Downgrowths from the inner, ventral corners of each segmental pouch extend for some distance into the splanchnocœl, and their walls give rise to the gonads. In embryos destined to become males hollow seminiferous tubules appear in the gonads, and they soon become extended laterally to establish communication with the mesonephric tubules. These composite tubules constitute the vasa efferentia, and across them sperms are conveyed to reach the exterior *viâ* the Wolffian ducts, often known in this connexion as the vasa deferentia.

The female makes no such use of the Wolffian ducts for the evacuation of eggs. Instead a new rod of cells is split off from the outer face of the somatopleur, and this becomes hollowed out to form a tube opening into the cloaca near the point of entry of the Wolffian duct. This tube is the Müllerian duct, and owing to its function of conveying eggs to the exterior it is known also as the oviduct.

Condition of Kidneys and Ducts in Gnathostomata. In the fish, exemplified by *Scyllium*, the adult kidney is a mesonephros. Excretory products are conveyed to the exterior by a Wolffian duct on either side. In the male the anterior mesonephric tubules are in connexion with the seminiferous tubules of the testes, thus forming a set of vasa efferentia in relation to each testis and the kidney of the same side. Sperms escape, therefore, *viâ* the Wolffian ducts. It is only the posterior portion of the mesonephros which remains actively excretory. The Müllerian ducts in the male are represented anteriorly by a pair of funnels ventral to the œsophagus, and posteriorly by a pair of sperm sacs. In other words, the extremities of the Müllerian ducts persist, whilst their intermediate portions have disappeared. In the female the whole of the mesonephros is excretory, and it plays no part in the evacuation of genital products. But the Müllerian ducts are well developed and function as oviducts, starting as a pair of funnels similar in position to those of the male. It is interesting to note that in *Scyllium* the cœlomostomes remain open, whilst the group to which this animal belongs is further peculiar in that the Müllerian duct arises by a longitudinal constriction of the Wolffian duct.

In the frog, characteristic of Amphibia, there is little advance on the condition in fish. A pronephros is the functional kidney of the early larva, but this later becomes replaced by a mesonephros, in connexion with the Wolffian ducts, which serve also for the conveyance of sperms to the exterior. Müllerian ducts arise to function as oviducts in the female, but disappear practically completely from the male. The cœlomostomes become closed, whilst a ventral evagination from the cloaca forms an urinary bladder. In some Amphibia—e.g. the newt—it is interesting to note that the tubules from the posterior (excretory) end of the mesonephros do not communicate with the Wolffian duct until the latter has almost reached the cloaca. Thus there is here expressed a tendency to the separation of excretory and genital functions even in the male, and in theory this could be completed if the mesonephric tubules never opened into the Wolffian duct at all but communicated direct with the cloaca.

In reptiles, birds and mammals the mesonephros is no longer the functional kidney in the adult, its place being taken by the metanephros. Its duct, the ureter, is a new structure, formed as an outgrowth from the posterior end of the Wolffian duct and growing forwards to penetrate the tissues of the metanephros. The term " ureter " should be confined exclusively to this structure, and not loosely employed for the urinary channels of lower forms. The condition of the ducts in *Lepus* may be taken as typical of mammals and birds. In the male the mesonephros is represented by the epididymis, partly surrounding the testis. Through this epididymis sperms pass into the vas deferens, which thus represents the Wolffian duct of lower forms. The only remnant of the Müllerian duct in the male is a small, blind diverticulum lying dorsal to the urinary bladder and known as the uterus masculinus. In the female the Müllerian ducts are represented by the oviducts, which unite to form a median vagina. The Wolffian ducts disappear completely, though traces of the mesonephros may be found in the form of the epoöphoron and the paroöphoron.

One or two peculiarities of the development of gonads in various forms may be recapitulated here. Thus in *Scyllium* and its allies only the right ovary persists, though both Müllerian ducts remain. In the bird there is found only a left ovary and oviduct. The testes of mammals arise within the body-cavity, but later descend into a scrotal sac.

Structure of Ovary and Testis. The ovary varies in structure to some extent amongst the different classes of Gnathostomata. The ovary is typically an hollow sac, cells in the wall of which eventually mature and give rise to ova, whilst other cells are absorbed as nourishment. The mammalian ovary is somewhat specialised. It consists of a small, almost solid mass of connective tissue, covered over by the germinal epithelium. From this latter invaginations pass into the substance of the ovary, and their ends are cut off to form little groups of cells. One of these cells becomes an egg, and is surrounded by the remainder in the form of an hollow sphere. These are secretory and liberate a liquid, in which floats the developing egg. The whole structure is called a Graafian follicle, and as the egg ripens this follicle approaches the surface of the ovary. Eventually it bursts and the egg is shed into the body-cavity. The ovary is penetrated by blood-vessels and nerve fibres, and some part of its mass is constituted by interstitial cells.

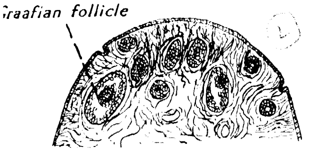


FIG. 172.—Transverse section of portion of mammalian ovary.

The testis is of comparatively uniform structure throughout the Gnathostomata. It consists of a large number of seminiferous tubules, each enveloped in connective tissue and with walls composed of germinal epithelium. From this sperm-mother cells are given off on the inside into the lumen of each tubule, where maturation occurs. The tubules are continuous with the vasa efferentia, through which sperms escape to reach the Wolffian ducts.

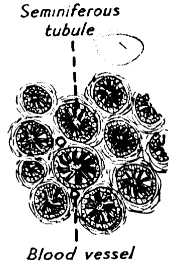


FIG. 173.—Section of portion of mammalian testis.

Cœlom and Mesoderm. The relation of the mesoderm and cœlomic cavity to the other organs of the body is typified in *Amphioxus*, and by a careful study of the embryology of that organism will this best be understood. It remains, therefore, to point out in what few respects there is found a departure from this primitive condition.

Even the ventral cœlom (splanchnocœl) is at first divided transversely by septa in *Amphioxus*, but these later disappear. In the

Gnathostomata they never appear at all, and the wall of this unsegmented region is called the lateral plate. The cœlomic cavities of the right and left sides do not become continuous dorsally, and the walls which separate them constitute the dorsal mesentery. The region on either side between the dorsal and ventral cœlom (myocœl and splanchnocœl respectively) is occupied by short, segmental stalks. In *Amphioxus* these form the gonads. In consequence they are known as gonotomes and their cavities as gonocœls. In Gnathostomata they give rise to the kidney tubules, and are known as nephrotomes : their cavities are the nephrocœls.

The splanchnocœl is interrupted by a pair of narrow, transverse septa in *Amphioxus*. In each of these runs a ductus Cuvieri. In the dogfish and its allies these septa divide a posterior peritoneal region of the splanchnocœl from an anterior pericardium, except for a pair of minute pericardio-peritoneal canals. In the remainder of the Gnathostomata the pericardium is completely closed off from the peritoneum.

As the gut becomes coiled and a number of diverticula is given off the cœlomic epithelium is bound to get considerably twisted and often secondary connexions occur with the formation of ligaments. Thus the lungs are covered by the pleura, whilst the cœlomic channel through which runs the bile duct is the **lesser omentum.** The pleura are often attached secondarily, by an accessory mesentery, to the roof of the peritoneum, whilst a connexion on either side between the pleura and the epithelium covering the liver constitutes the **pulmohepatic ligament.** But one of the main features causing the complication of the cœlomic cavity is the invariable kink to the right made by the stomach. In this region the dorsal mesentery is called the **great omentum,** and as a result of the bending forwards of the gut forms a sac, the **omental bursa.** This opens into the peritoneum by the **foramen of Winslow.** The presence of the diaphragm in mammals has already been referred to (page 199). It is formed partly from the transverse septum and partly from epithelium associated with the mesenteries supporting the early kidneys. Through this diaphragm pass the œsophagus, the dorsal aorta and the posterior vena cava.

Thus the cœlom is essentially a cavity, bordered on its inner and outer sides by mesoderm, and in which the soft organs of the trunk are suspended. The cavity contains a fluid, so that the viscera are to some extent protected from mechanical shock. The cœlomic wall becomes modified dorsally, the median wall giving rise to the myotome of its own segment and the lateral wall to the dermis. Secondary spaces arise in the mesoderm, forming blood-vessels, whilst from the nephrotomes are developed the kidney tubules.

CHAPTER XXIII

NERVOUS SYSTEM AND SENSE ORGANS

THE nervous system of Chordata is built on a definite plan, and differs only in the extent of specialisation of various parts, especially of the brain, in all the groups comprising this phylum.

Plan of Nervous System. The nervous system is essentially divisible into a central nervous system and a peripheral nervous system, the former consisting of brain and spinal cord, and the latter of a number of pairs of cranial and spinal nerves. The structure and relationship of these various organs has already been described for each type, and it remains now to consider the way in which nervous integration is effected.

Reflex Arc and Reflex Action. The majority of actions performed by any member of the Chordata are comparatively complex, and it is now necessary to inquire whether or not they can be resolved into simpler components. In order to do this it is essential to study in detail the structure of the spinal cord, and for this purpose it will be imagined that a transverse section of this organ has been cut in a region where a spinal nerve enters it. It must be clearly realised at the outset that a single nerve, as seen in dissection, is really a bundle of some hundreds of axons (page 166), all enclosed in a common sheath. For the sake of simplicity only

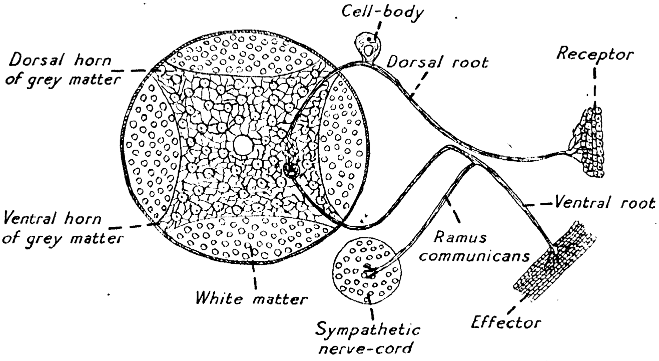


FIG. 174.—Transverse section of spinal cord at point of entry of spinal nerve.

two of these axons will be considered. Let it be imagined that the skin of the hand is irritated. This means that the skin of that region receives a nervous message, known as a stimulus. It is therefore described as a receptor organ. This stimulus passes up the arm *viâ* an axon into the spinal cord. The axon along which such a stimulus is conducted is observed to penetrate the dorsal horn of the grey matter of the spinal cord. It is therefore called a dorsal root. Its cell-body occurs just outside the spinal cord, so that this particular nerve cell has two axons—one reaching from the hand to the cell-body and the other extending from the cell-body to the grey matter of the spinal cord. Consequently it is described as bi-polar. Since this dorsal root carries messages from the receptor organ into the spinal cord it is described as afferent, or alternatively it is said to be a sensory nerve fibre. Once within the grey matter the axon becomes subdivided to form a terminal arborisation. The branches thus produced establish contact with the dendrites of several cell-bodies, but, for the sake of simplicity again, only one such will be considered. This region of contact between terminal arborisation and dendrites is known as a synapse. The cell-body in question now gives off an axon. This emerges from the spinal cord through the ventral horn of the grey matter. Immediately it travels in a dorsal direction and runs for some distance in company with the dorsal root already mentioned. Soon it separates from it again, and, having done so, gives off a short branch known as a ramus communicans to join the sympathetic nerve-cord. The ventral root itself passes to some muscle of the arm and stimulates it to contract, so that the hand is moved from the source of irritation. This muscle is therefore called an effector organ. The ventral root, since it conveys stimuli away from the spinal cord, is known as efferent, or alternatively it is said to be a motor nerve fibre. The above is the simplest form of nervous path which can be depicted, and is called a reflex arc. To recapitulate, the component organs of a reflex arc are the receptor organ, connected with the grey matter of the spinal cord by a dorsal root. In the grey matter this forms a synapse with the ventral root, which in turn carries the stimulus out to an effector organ, giving off *en route* a ramus communicans to the sympathetic nerve-cord. The action thus accommodated is said to be a reflex action. It takes place without reference to the brain, and the message passes out of the grey matter at the same level of the spinal cord as that at which it entered—i.e. its only motion in the spinal cord is from the dorsal to the ventral surface : it is not carried in an anterior or posterior direction. This simple nervous path is often described as the unit of nervous integration, for the majority of actions may be accounted for by a modified form of this simple mechanism, and where this is impossible it may be assumed that our inability so to do is due to lack of knowledge either of the stimulus bringing forth a given reaction or of the connexions which are effected in the synapses of the central nervous system. In other words the sum total of the reactions of the body fall into simple categories of cause and effect.

Association Neurones. Now let it be imagined that the stimulus be applied to the upper part of the hind-leg of an animal, such that the fore-limb must be brought into action to remove the source of irritation. The receptor organ lies in the skin of the leg, and from this a dorsal root conveys the stimulus into the grey matter at the base of the spinal cord. Here the dorsal root forms a synapse with the dendrites of a nerve cell. But the axon of the latter cell, instead of passing out again into the leg, enters the white matter of the spinal cord, and in it runs to the level of the fore-leg. Here it plunges again into the grey matter and breaks up to form a terminal arborisation. This forms a synapse with the dendrites of a true ventral root, whose axon emerges from the ventral horn of the grey matter to pass to the muscles of the fore-leg. The nerve cell whose axon connects the dorsal root at the base of the spinal cord with the ventral root at the level of the fore-leg is known as an association neurone. It is by means of association neurones that stimuli are conveyed up and down the spinal cord. Such nervous action as that described above is clearly a modification of the simple reflex action.

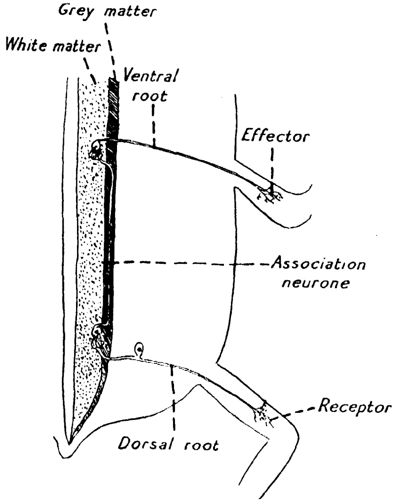


FIG. 175.—Longitudinal section of spinal cord.

White and Grey Matter. It will have been observed that a dorsal root always enters the grey matter by the dorsal horn, whilst a ventral root emerges from the same part of the spinal cord by the ventral horn. Thus the grey matter consists of the terminal arborisations of the dorsal roots, cell-bodies and dendrites of ventral roots, and the synapses between them. When a message is to be transferred up or down the spinal cord this is effected by an association neurone, the axon of which travels in the white matter.

Thus the white matter is composed merely of axons of association neurones running in a longitudinal direction. In transverse section, therefore, the grey matter consists of a mass of closely-packed nervous tissue, whereas in the white matter may be seen merely the cut edges of the axons. The grey matter is therefore more opaque than the white matter.

Structure of a Spinal Nerve. A single spinal nerve consists of some hundreds of axons of dorsal roots and an approximately equal number of axons of ventral roots. Each dorsal root axon bears a cell-body just outside the spinal cord, so that at this point there occurs a mass of cell-bodies. This constitutes the dorsal root ganglion and is visible externally as a swelling. Only for a short distance does the bunch of ventral root axons run with that of dorsal root axons. Each ventral root axon is in association with a ramus communicans, so that the structure identified in dissection and known by this name is in reality a mass of nerve fibres. The farther the nerve passes from the spinal cord the thinner it becomes, for individual axons are continually leaving it to supply organs immediately surrounding the nerve.

Nervous and Telephone Messages. Should any doubt still exist with regard to the principle on which nervous messages are transferred from one part of the body to the other they may probably be dispelled by a careful comparison between such messages and conversations directed by telephone. The simple reflex arc may be closely compared to a local telephone call. The receptor organ corresponds to the speaking tube of the telephone lodged with the sender of the call. The nervous message is conveyed along the dorsal root to the grey matter of the spinal cord, where, in the form of a synapse, it establishes connexion with the cell-body of the ventral root. Similarly the telephone message is passed along a conducting wire to the nearest telephone exchange, where electrical connexions are completed, either automatically or by an operator. The nervous message is then carried along the ventral root to the effector organ, whilst the telephone message is carried along a further conducting wire to the receiver.

The more complicated type of passage of a nervous message, involving the use of an association neurone, may be compared in like manner to a trunk call by telephone. The origin of the messages is the same as before, the nervous message thus reaching the grey matter of the spinal cord and the telephone message the local exchange. The nervous stimulus is now passed along the association neurone to reach the cell-body of the ventral root. This corresponds to the passage of the telephone message from the local exchange to the one nearest the intended destination of the message. Finally the nervous message is passed along the ventral root to the effector organ, and the telephone message from the second exchange to the receiver.

Cranial Nerves and Segmentation of the Head. It has already been observed that a typical spinal nerve consists of a dorsal root and a ventral root, working in close association. The former is concerned with the reception of stimuli and their conveyance to the spinal cord, whereas the latter redistributes them to the musculature of that particular segment. Thus in the trunk segmentation is a fairly obvious phenomenon, since it is manifest in both the disposition of the spinal nerves and the transverse division of the vertebral column into separate vertebræ. But this same phenomenon is by no means so apparent as a result of a cursory survey of the structure of the head. No segmental arrangement is demonstrated either by the skull or by the distribution of the cranial nerves.

One characteristic of cranial nerves, in which they differ from spinals, is that each is either a dorsal root or a ventral root, but they never join to form mixed nerves. By tracing the development of cranial nerves and drawing comparisons between various types it has been found possible to establish the following degree of segmentation in the head of *Scyllium*, and with but slight modifications the results are applicable to other Craniata.

The first and second cranial nerves (the olfactory and the optic) are not true nerves, and are therefore of no significance in this respect. No. I is formed by the backward extension of processes from cells constituting the epithelium lining the nasal chambers. These processes penetrate the olfactory lobes and comprise the olfactory nerves. No. II is formed, as is the whole eye-cup, merely by an outgrowth from the mesencephalon itself.

The first true segment, known as the premandibular, has for its dorsal root the profundus branch of the trigeminal nerve. Unfortunately this disappears in *Scyllium*, but is present in closely-related forms. The ventral root corresponding to this is the occulomotor nerve (III).

The second (mandibular) segment has as its dorsal root the remainder of the trigeminal nerve (V)—i.e. the superficial ophthalmic maxillary and mandibular branches. Nerve IV (trochlear) is the corresponding ventral root.

The third segment is known as the hyoid, and the facial nerve (VII) supplies its dorsal root, whilst the auditory nerve is regarded as a branch of this. It has for its ventral root the abducens nerve (VI).

The fourth segment has as its dorsal root the glossopharyngeal

(IX), whilst the disappearance of the myotome from this segment accounts for the absence of the corresponding ventral root.

The vagus nerve supplies the dorsal roots of the fifth, sixth, seventh and eighth segments. The myotome of the fifth segment disappears, so that, like the fourth segment, this has no ventral root. The ventral roots of the sixth, seventh and eighth segments are provided by the hypoglossal nerve. In the dogfish this is not a cranial nerve, since it arises outside the skull. In reptiles, birds and mammals, however, its origin comes to lie within the skull, and thus it constitutes the twelfth cranial nerve, whilst the eleventh, known as the spinal accessory, is a specialised branch of the vagus. Thus the ninth segment of the body is the first to have a complete, mixed spinal nerve. It is characteristic of each dorsal root that it bears a ganglion—i.e. the Gasserian, geniculate, petrosal and vagus ganglia of nerves V, VII, IX and X respectively—and it innervates a sensory surface. The ventral roots have no ganglia, and each supplies the musculature of its own segment.

The following table will serve as a summary of the segmentation of the head, almost completely applicable to *Scyllium*, indicating nervous supply and the positions of the visceral arches and gill-slits :

Segment	Visceral Arch	Gill-slit	Dorsal Root	Ventral Root
1			V (Prof.)	III
2	Mandibular		V (others)	IV
		Spiracle		
3	Hyoid		VII	VI
		1st		
4	1st branchial		IX	—
		2nd		
5	2nd branchial		X	—
		3rd		
6	3rd branchial		X	Hypoglossal
		4th		
7	4th branchial		X	Hypoglossal
		5th		
8	5th branchial		X	Hypoglossal

Components of Nerves. According to their function nerves may be separated into four classes. There are those nerves which convey stimuli from the outside world to the central nervous system of the animal ; they are described as somatic sensory nerves. Others carry messages from some region within the body to the central nervous system, and are therefore known as visceral sensory nerves. The remaining two classes of nerves are those conveying stimuli away from the central nervous system. Somatic motor nerves run to striped (voluntary) muscles of the body, and visceral motor to the unstriped (involuntary) muscles. The dorsal root of a spinal nerve is almost entirely somatic sensory, whilst the ventral root is somatic motor. In the associated ramus communicans run both visceral sensory and visceral motor components. There is one part of the somatic sensory system clearly differentiated from the remainder, yet of great importance to the organism. The voluntary muscles of the body are supplied not only by efferent fibres, but also by afferent. Imagine that a man is stimulated to bend his arm. This means that the biceps muscle must contract. Not only so, but the extensor muscle, running behind the elbow joint, must relax to allow this movement. This is made possible by the passage of a stimulus *from* the biceps muscle into the central nervous system and back to the extensor muscle, which is thus stimulated to relax. Such a nerve as that leaving the biceps muscle for the central nervous system is known as a proprioceptor. The importance of the proprioceptive system will at once be apparent if the complicated muscular activity involved in walking be analysed, for here not only must the various muscles of each leg be co-ordinated, but the relative positions of the two legs must also be correlated. Thus the ear is of importance in connexion with the proprioceptive system, for it regulates the movements responsible for the maintenance of equilibrium.

Brain. It will be apparent that the spinal cord can receive from the outside world stimuli of one type only, namely, that of touch. Such stimuli are severely limited in number, for each can be applied only by definite contact with the surface of the body. But at the front end of the body are found the sense organs, and these can receive stimuli from a distance. It is true that smelling is due to contact of particles of the odoriferous substance with the nasal epithelium, but molecules will suffice to bring about the impression of smell, though the bulk of the substance be at a considerable distance from the body. Hearing and sight are due merely to vibrations, and can thus be transmitted for a very great distance. Accordingly the eyes, nasal organs and ears are known as distance receptors, since they receive a stimulus at a distance from its source. Thus in the head region there have to be received a very great many more stimuli than elsewhere, so that accordingly specialised centres are developed to accommodate this demand. They are the optic lobes (sight), olfactory lobes (smell) and some part of the medulla (hearing). The question left to be solved is why this specialisation should occur at the front end of the body. The answer is not far to seek, for this is the end which normally leads in progression. Having the distance receptors at the front end of the body the animal becomes aware of environmental conditions at the earliest possible moment.

Centres of the Brain. The regions of the brain where the various stimuli are received are known as nerve-centres. Thus, in the dogfish there is little left of the brain once these centres are removed. Stimuli from the skin and ear pass to the medulla, from the eyes to the optic lobes, and from the nasal epithelium to the large olfactory lobes. There is, however, very little correlation between them. Only the cerebellum remains of any importance. To some extent this organ succeeds in correlating auditory and visual stimuli, for it receives from the ear messages as to orientation of the body in space, from the eye it learns the position of the body relative to external objects, whilst proprioceptive nerve fibres acquaint it of the state of contraction or relaxation of the muscles of the body. Thus the cerebellum becomes the chief centre of the proprioceptive system, and regulates posture and movement of the body.

Correlation Centres. In forms above the fish other correlation centres, in addition to the cerebellum, become well developed. Thus the walls of the diencephalon become thickened to form the optic thalami, the floor of the telencephalon forms the corpus striatum, whilst the roof of this region becomes very much enlarged to form the cerebral hemispheres.

The thalami receive stimuli from all the sense-centres, and one of its most important functions is their analysis into pleasurable and painful. Accordingly it determines whether a negative reaction shall result, as an escape from danger, or a positive one, as an advance towards food.

The corpus striatum is very important in birds, and it has already been referred to (page 212) in relation to the important part it plays in accommodating the instinctive movements performed by the bird in its migratory habits. As previously pointed out, the detailed structure of this organ is as much a part of the hereditary constitution of the bird as is the colour of its plumage. The structure of the corpus striatum would appear to be more or less irrevocably determined, and little or no plasticity remains in regard to the formation of alternative synaptic connexions. Thus a bird is capable of carrying out purely instinctive reactions, but is quite unable to adapt itself to any novel set of circumstances. Thus it can learn remarkably little by experience.

The cerebral hemispheres are almost completely absent in fish. In Amphibia the neurones composing them immediately surround the lateral ventricles. Thus the grey matter, constituted by the synaptic connexions between these neurones, occupies the same position as in the spinal cord. A few of the neurones, however, do migrate towards the surface. In reptiles this migration has taken place to a greater extent, so that there is now a superficial layer of grey matter covering each cerebral hemisphere. This is divisible into three regions, two of which are concerned with the reception of stimuli from the olfactory lobes. This is no doubt due to the fact that they are the nearest of the sense-centres to the cerebral hemispheres. These two centres constitute the archipallium, whilst a small region, known as the neopallium, receives messages equally from all the sense-centres. It is this region which becomes most highly developed in mammals.

The cerebral cortex, as the superficial layer of grey matter covering the cerebral hemispheres now becomes known, is but poorly represented in birds. This may be explained on the grounds that they are sufficiently masters of their environment as a result of the very high degree of perfection to which their instinctive behaviour is developed, accommodated by the corpus striatum.

The cerebral cortex in mammals becomes enormously enlarged, mostly as a result of being thrown into copious folds. That of each side is connected with the other by a transverse band of fibres, known as the corpus callosum. It is connected directly and indirectly with all the sense-centres, and the number of neurones in the human cerebral cortex is in the neighbourhood of ten million. Large as is this number it has to be remembered that the number of possible connexions which may be established between them is so great as to be beyond comprehension. The synapses between these neurones are not so arranged that the path of a stimulus is predetermined as it is in birds. The key-note of the structure of the cerebral cortex is its plasticity. The function of this organ is to receive stimuli from the various sense-centres and elicit the best response to all the stimuli considered collectively. Thus predetermined behaviour gives place in mammals to a certain arbitrary choice and judgement. There is no necessity to invoke the existence of a will to account for the complicated response to stimuli, even in the human. Only through our ignorance of the internal workings of the cerebral cortex, or even through our failure to recognise external stimuli, are we baffled by the way in which human behaviour appears to differ from that even of lower mammals. But if only one (of the ten) million neurones in the cerebral cortex be considered, then the number of possible combinations between any two of them is expressed by a number with some three million figures in it. Small wonder that human actions cannot always be readily explained in terms of stimulus and response! Yet definite tracts may be established in this cerebral cortex, and the whole of education, taken in the wide sense of the sum-total of all personal experience, consists of the establishment in more or less permanent form of certain of these tracts. Thus the learning of a poem may be taken as an example. The articulation of each word may be regarded as the stimulus calling forth the next word, and the whole as due to the passage of the nervous stimulus in a definite order through the neurones of the cerebral cortex, and from them to the muscles responsible for speech. The plasticity of the cerebral cortex enables mammals to adapt themselves to novel conditions, for each such condition will elicit some new response, since it is a new stimulus.

In connexion with the acquisition of definite tracts in the cerebral cortex as a result of education in the human it is very important to realise the part played by speech and writing. By this means an individual is able, not only to learn from his own personal experience, but also to acquire a great deal of experience ready-made from his contemporaries and predecessors in infinitely less time than he could discover it all for himself, so that his responses to stimuli become accordingly modified. This knowledge of what another has done in certain circumstances becomes registered in his own cerebral cortex, so that he may behave similarly if the same set of circumstances crops up in his own experience. It is not to be wondered at, therefore, that a species in which these attributes have been so highly developed as they are in man should be the present peak of evolutionary progress.

Autonomic Nervous System. The term "sympathetic" nervous system is usually rather loosely employed to cover the whole of the efferent supply to the viscera, but this is misleading. It is properly known as the autonomic nervous system, and is composed of a sympathetic and a parasympathetic system. The former is confined to the thoracic and lumbar regions, and the latter to the head and sacrum. It is characteristic of the whole system that, while it is essentially effector, fibres do not reach all the way from the grey matter of the central nervous system to the involuntary muscle or gland to be stimulated, but somewhere or other form a synaptic connexion, usually in one of the sympathetic ganglia.

(A) SYMPATHETIC SYSTEM. Leaving the grey matter of the nerve-cord in close association with the ventral roots of the spinal nerves are the neurones constituting the rami communicantes, having their cell-bodies within the grey matter. Each passes into a sympathetic ganglion of its own side. Here it may form a synapse, or alternatively it may travel through this ganglion to the one immediately in front of or behind it before establishing a synaptic connexion. In this way a slender chain is formed connecting the ganglia. The neurone thus running from the grey matter of the nerve-cord to the sympathetic ganglion is known as a connector neurone, whilst the one with which it forms a synapse in the ganglion is called the effector neurone. This latter has its cell-body in the sympathetic ganglion, from which it passes to stimulate some involuntary muscle or gland. Alternatively the two neurones constituting such an efferent circuit may be described as preganglionic and postganglionic respectively. Occasionally the preganglionic neurone runs straight through the sympathetic ganglion to others situated near the bases of the cœliac and mesenteric arteries. So long and distinct are they that they are known as splanchnic nerves. When they reach their ganglia they form synapses, just as the others do, in the sympathetic ganglia.

(B) PARASYMPATHETIC SYSTEM. This consists of fibres arising from the head and sacral region, and all of them form synapses in ganglia situated on the organs which they stimulate, so that there is no parasympathetic nerve-cord formed. The parasympathetic fibres from the sacral region unite to form the pelvic nerves, whilst the course of fibres from the head is considerably complicated.

(C) FUNCTIONS. Sympathetic and parasympathetic fibres supply the same organs, but the effects of their stimulation are of opposite nature. Muscles caused to contract by sympathetic stimulation will relax under the influence of parasympathetic activation, but co-ordination is effected between them.

The autonomic nervous system is not represented in *Amphioxus*, but appears in all higher Chordata.

Sense Organs. It remains in conclusion briefly to compare the extent to which the nasal organs, eyes and ears have been developed in the various classes of the Gnathostomata.

(A) NASAL ORGANS. In all classes this takes the form of a pair of sacs lined with a sensitive epithelium, processes from the cells of which have become extended backwards to form the olfactory nerves, penetrating the olfactory lobes. In the dogfish, as in all fish except the Dipnoi, these nasal chambers do not communicate with the mouth. This is only to be expected in view of the mode of respiration in fish. In the Dipnoi and in the remaining four classes of Gnathostomata there is open communication between the nasal cavities and the mouth, so that a pair of important respiratory channels is formed. The nasal cavities themselves differ from the condition in the dogfish only in mammals, where the epithelium has become subdivided to such an extent that special scroll-like, turbinal bones are developed to support it.

In connexion with the nasal organs of all land vertebrates a pair of pouches, known as Jacobson's organs, is developed. They arise ventral to the nasal cavities, and open each by an independent aperture into the mouth. In some forms, including man, they have become secondarily lost.

(B) EYES. The eyes of all the Chordata are essentially similar in structure. The most important respect in which they differ from each other is that of accommodation for the focussing of objects at various distances. This is done either by the alteration of the focal length of the lens or by its movement nearer to or further away from the retina, for vision depends on the throwing on to the retina an image of the object looked at.

In fish very little accommodation is possible. This would be expected, in view of the comparative opacity of the medium in which they live. The bony fish (Ostiechthyes) can vary to some slight extent the distance between the retina and the lens by the drawing of the lens inwards, thus enabling objects at a greater distance to be focussed.

In Amphibia the position is reversed, for under normal circumstances the eye is focussed to form an image of a distant object. The lens is therefore moved forwards when a nearer object is to be focussed.

In the remaining classes the focal length of the lens is varied. Thus in reptiles the lens is contracted, so that its focal length is decreased, when near objects are to be viewed, whilst in birds this same type of accommodation is further assisted by an increase in the convexity of the cornea.

In mammals the same effect as in reptiles is produced, but in a different manner. The lens is held in position by attachment to a pair of ciliary processes. Now the ciliary muscle is attached to the cornea in front and to the choroid layer of the eye just behind the ciliary process. When this muscle contracts the ciliary processes are drawn forwards and therefore inwards. The lens then becomes more spherical of its own accord, for it is of such a shape and consistency that it is prevented from becoming completely spherical only by its attachment top and bottom to the ciliary processes. With this increased convexity nearer objects can be focussed.

It will be realised that with the form of optical arrangement found in the vertebrate eye the image thrown on to the retina must be an inverted one. This is presumably re-inverted during its passage through the optic nerve before translation in the optic lobes as a visual impression.

A peculiarity of many mammals is the possession of stereoscopic vision. By this it is implied that both eyes are focussed simultaneously on the same object. This is of great importance in the estimation of distance. It is, of course, essential in such cases that co-ordination between the muscles of the two eyes should be extremely highly developed. The advantages of stereoscopic vision are to some extent neutralised by the fact that the field of vision is very greatly reduced.

In conclusion the structure of the retina must be considered. Running over the surface of the retina are the fibres of the optic nerve. These establish connexions with the neurones running near the surface of the retina. These in turn form synaptic connexions with the light-sensitive cells, occupying only about the innermost sixth of the total thickness of the retina. Some of these sensitive cells end in the form of rods, whilst others terminate in conical projections. Accordingly the cells are known as the **rods** and **cones** of the retina. It has been suggested that the latter are responsible for colour perception, whilst the former distinguish various intensities of light. This is largely presumed from the comparative scarcity of cones in animals where colour perception is unlikely to exist, as in nocturnal forms. It is observed also that the number of cones is greater in the higher vertebrates than in the lower. The perception of colour is doubtless due to the varying effects of stimulation of the sensitive cells of the retina by lights of different wave-lengths, whilst light of wave-length outside certain quite wide limits is not perceived at all. Just above the **blind spot,** where the optic nerve penetrates the retina and where no light can be perceived, is an especially sensitive region of the retina, known as the **yellow spot** on account of its characteristic colour. The centre of this region, known as the **fovea centralis,** is characterised by the thinning out of the cells of the retina, whilst the only sensitive cells present are the cones. When an object is being looked at intently it is believed to be focussed on to this fovea centralis.

(C) EARS. The ear is formed essentially by an ectodermal invagination, forming a sac known as the utriculus. This becomes further modified by the outgrowth of three semi-circular canals and a ventral sacculus. Each canal communicates at both ends with the utriculus, whilst at one end it becomes enlarged to form an ampulla. This contains statoliths in the form of small particles of calcareous material, held in a mucous secretion. These are supported on sensory hairs, so that movement by the animal from its normal position in space is registered, and adjustments are made. This primitive part of the ear thus functions as an organ of balance. The connexion with the exterior is retained in the dogfish in the form of the ductus endolymphaticus. The whole ear is filled with endolymph and is supported in the auditory capsule by perilymph.

In terrestrial vertebrates the function of hearing becomes an important attribute of the ear. At the same time the spiracle no longer serves any respiratory purpose, so that it becomes the Eustachian tube, closed off from the exterior by the tympanum. Accordingly the hyomandibula, since the hyostylic mode of attachment of the jaws has been replaced by the autostylic, now becomes the columella auris, connecting the tympanum with the membrane across the opening of the auditory capsule, known as the fenestra ovalis. This condition is found in the frog, and persists throughout the remaining classes of the Gnathostomata except the mammals. Here there are three bones, known collectively as the auditory ossicles, connecting the tympanum with the fenestra ovalis. They are the stapes next the fenestra ovalis and homologous with the columella auris (hyomandibula) of lower forms, the incus and malleus, homologous respectively with the quadrate and articular. The function of hearing is accommodated in the cochlea. This is rudimentary in the Amphibia, but becomes more highly developed in the other classes.

(D) TASTE ORGANS. These are stimulated by contact with particles of the substance tasted. In terrestrial verbebrates they are confined to the mouth, but in fish may be found elsewhere on the surface of the body. A single taste-bud, many of which occur on the tongue, consists of a mass of non-sensory cells enclosing a number of sensitive cells, from each of which projects a minute process into the cavity of the mouth. At their inner extremities these cells are innervated by visceral afferent fibres, which reach the medulla through the facial, glossopharyngeal and vagus nerves.

CHAPTER XXIV

SKELETON AND SKIN

SKELETON

THE body of a Chordate is supported primitively by an elastic notochord, extending throughout the length of the animal and situated immediately beneath the nerve-cord. It is of endodermal origin, and this condition is represented in *Amphioxus*. In this genus the median fins are supported by fin-rays of mesodermal origin, whilst paired fins are absent. In the Gnathostomata the notochord becomes more or less completely replaced by cartilage or bone, whilst limb-girdles are developed for the attachment of the paired limbs. In this way a vertebral column is formed, enclosing the nerve-cord. At the anterior end this cartilaginous or bony case becomes specially modified to form the skull, in which is contained the brain. Each part of the skeleton will now be considered individually.

Vertebral Column. In the dogfish and its allies a complete vertebral column first appears. It consists of a number of ring-shaped vertebræ placed together end to end. Each is formed dorsally by a pair of basidorsals, and ventrally by a pair of basiventrals. The upper parts of the basidorsals constitute the neural arches, and these meet in the mid-dorsal line to enclose a tube through which passes the nerve-cord. The centrum of each vertebra is formed of the lower portions of the pair of basidorsals and the upper portions of the pair of basiventrals. In the region of the tail the lower portions of the basiventrals constitute the hæmal arches. The basidorsals are separated by interdorsals and the basiventrals by interventrals. The notochord itself thus becomes almost completely replaced by cartilage, except for very thin intervertebral discs between the centra.

In higher forms—i.e. from the Osteichthyes (except Dipnoi) upwards—the notochord becomes completely replaced by bone. A further modification occurs in that the basidorsals and basiventrals of each segment become fused on to the interdorsals and interventrals immediately behind. In consequence the vertebræ come to be intersegmental structures, so that the muscle-blocks (myotomes) are each connected to two vertebræ. Between every two successive vertebræ a pair of foramina is enclosed for the egress of the segmental spinal nerves. Primitively these bony vertebræ possessed two centra, an anterior one formed from the pair of basiventrals and called the hypocentrum, and a posterior one formed from the basiventrals and the lower portion of the basidorsals and called the pleurocentrum. In Amphibia the hypocentrum is enlarged at the expense of the pleurocentrum, whereas in higher classes the reverse has occurred. Accordingly in Amphibia the hæmal arches occur as outgrowths of the centra themselves, since these are essentially developed from the basiventrals. But in reptiles, birds and mammals they arise from small bones, called intercentra, which in reality represent the hypocentra of Amphibia. In forms where they exist they are known as chevron bones. Transverse processes are lateral extensions of the basidorsals, occurring at the base of the neural arches and serving for the attachment of muscles. Special facets, known as anterior and posterior zygapophyses, are developed for articulation. In shape vertebræ are normally concave behind and convex in front, whilst the peculiar heterocœlous condition of the cervical vertebræ in birds has already been referred to (page 208). Primitively the vertebræ comprising the vertebral column are of similar structure throughout, but in the higher forms a certain amount of regional differentiation has occurred.

Ribs and Sternum. Ribs are formed as outgrowths of the basiventrals. They come to articulate dorsally with the centrum by a double head, the tuberculum with the transverse process and the capitulum with the centrum, though primitively these two processes are not distinguishable. In the cervical region the ribs become completely fused with the vertebræ, enclosing on each side a vertebrarterial canal. Ribs extend ventrally to unite with the sternum, except for those which end freely and are called floating ribs. The sternum in Amphibia, as in higher forms, arises from paired rudiments, originally of cartilage but later invaded to form cartilage-bone. In modern Amphibia there is no connexion between the ribs and sternum, but this condition is probably secondary. The sternum is usually connected also with the elements of the pectoral girdle, as well as which it bears posteriorly an enlarged keel. This is especially important in birds, where it serves for attachment of the pectoralis muscles.

Limbs. The most primitive locomotory organs of the Gnathostomata are probably the median fins, which may be imagined to have extended throughout the greater part of the length of the animal and to have been continuous posteriorly, thus constituting a tail fin. But the most important organs are the paired fins, pectoral and pelvic, since it is from them that the paired limbs of the Tetrapoda have emerged. It has been suggested that these too, like the median fins, were at one time continuous, lateral folds of the body-wall, and have since become separated by the disappearance of the intermediate regions. Each such fin is developed as a fold in the body-wall, and into it extend muscle-buds. Cartilaginous radials are formed, and primitively the fins are of the same width throughout. Later, however, the radials became concentrated at the base, so that the fin appeared to be expanded distally. In addition to the cartilaginous radials dermal fin-rays are developed to articulate with them. In fact in the Osteichthyes these form almost the sole support of the fins. By a reduction in the number of radials and elongation of the basal (proximal) ones it is possible to imagine that the Tetrapod limb arose. The earliest of these probably contained more than five digits. Primitively they served to move the animal along on land, whilst its ventral surface rested on the ground. This meant that the limbs occupied a more or less horizontal position. But later the body became raised from the ground. This involved a right-angled bend at the first (knee and elbow) joints, so that the lower part of the limb was now placed vertically. At the wrist and ankle another right-angled bend was necessary so that the foot and hand could rest flat on the ground. In mammals further rotation of various parts of the limbs has occurred. The hind limb has been rotated forwards in a right angle from the hip joint. Thus the thigh runs in an anterior direction, the lower leg pointing vertically downwards and the foot remaining flat on the ground. The upper arm, instead of running out vertical to the body, is now directed backwards. This means that it has been rotated backwards through a right angle. But the hand points forwards, so that at the wrist joint rotation through two right angles must have occurred. This reasoning can readily be followed if the student adopts a squatting position and, bearing in mind the primitive condition, compares it with the orientation of the various regions of his own limbs. Many higher mammals have a certain degree of freedom in regard to the orientation of the lower part of the arm. Thus positions of pronation or supination (page 180) may be assumed.

Various forms of adaptation to locomotion on land may be noticed. Thus in such animals as the dog the foot rests on the under surface of the digits, the remainder being raised from the ground. In the horse and cow the foot is in contact with the ground only by the end joints of certain digits. In the horse this is the third, the second and fourth metacarpals and metatarsals remaining only as vestiges and constituting the splint-bones. The fossil-history of the horse shows the development of this condition from *Eohippus*, where four well formed digits and a vestigial fifth were present, through *Orohippus*, *Mesohippus* and *Protohippus* to the modern *Equus*. It is a remarkable instance of convergent evolution that a similar but obviously independent process has occurred in the ancestral history of cattle. Here the third and fourth digits remain, so that the animal is cloven-hoofed. Forms like the horse, where one digit remains, are known as Perissodactyls, whilst the cloven-hoofed types are the Artiodactyls. Curiously enough the primitive pentadactyl condition—i.e. having five digits—is preserved best in the most specialised group of mammals, namely the Primates. In Apes the first digit of the foot, as well as that of the hand, is capable of working in conjunction with the remainder to render these organs prehensile, whilst in man only the hand can function in this way.

In a study of adaptation to aerial locomotion further cases of convergent evolution are found, for flight has been developed independently by three groups, and their wings differ essentially in structure, but function similarly. Thus in extinct flying reptiles (Pterosaurs) it was the fourth digit which became very much elongated to support a fold of skin extending from the lateral surface of the body and constituting the wing. In birds there remain only three digits in the anterior limb, and these are without claws. The wing is formed by an outgrowth of a number of feathers from the tissue covering these and the fore-arm. The digits of the fore-limb of the fossil bird, *Archæornis*, were much longer than those of the modern bird, and bore large claws.

In a similar manner convergent evolution has taken place amongst the primitively terrestrial forms which have reassumed an aquatic mode of life. Whales, seals, penguins and turtles may be mentioned as examples. Here the limbs become modified to form paddles, and superficially they resemble the fins of fish.

Finally it may be mentioned that in certain cases limbs have been lost completely. Examples of this are afforded by snakes and certain Amphibia (Gymnophiona).

Limb-girdles. In accordance with the development of paired locomotory organs skeletal attachments become necessary for the muscles connected with them. Thus the pectoral and pelvic girdles become developed, probably from the radials at the base of the fins.

(A) PECTORAL GIRDLE. This consists essentially of a dorsal scapular and a ventral coracoid region. These become ossified to form cartilage-bones, and a number of dermal bones is found associated with them in the Osteichthyes, the most important being the clavicle. The reason for this latter development is that in the region of the gill-slits the body-wall is weakened by so many perforations, so that a dermal skeleton becomes developed there for the attachment of muscles of that region. Only secondarily does it become connected with the cartilaginous pectoral girdle. This theory is supported by the fact that no dermal bones are developed in relation to the pelvic girdle. Primitively there was no connexion between the pectoral girdle and any other part of the skeleton. In the Tetrapoda the pectoral girdle comes to rest on the ribs, whilst in the Amphibia it forms an almost complete hoop of bone to support the body-wall, as in the frog, in connexion ventrally with the sternum. In the Amniota membrane-bones are represented only by a clavicle and interclavicle, the latter being joined to the anterior end of the sternum. In mammals the interclavicle has disappeared except in such forms as *Ornithorhynchus* (platypus). The importance of the pectoral girdle as a support for the anterior part of the body-wall becomes reduced as ribs extend ventrally in the latter from the vertebral column to the sternum. Accordingly the pectoral girdle becomes separated into two completely independent halves in birds and mammals, except that the clavicles of birds are united in the middle line. In mammals the clavicle connects the acromion process with the sternum, whilst the coracoid has become reduced to a small process at the ventral edge of the scapula.

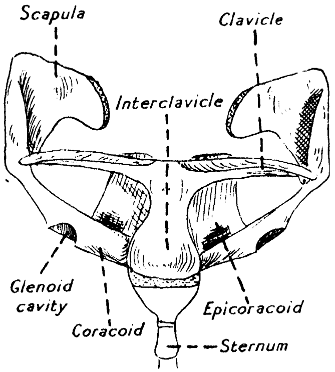


FIG. 176.—*Ornithorhynchus.* Pectoral girdle.

(B) PELVIC GIRDLE. This consists essentially in all the Tetrapoda of an ilium on each side extending forwards to become firmly attached to the fused sacral vertebræ. It is continued backwards as the ischium, whilst the pubis unites with both bones to form part of the margin of the acetabulum, into which fits the head of the femur. This condition may be well seen in the frog, where the two halves of the girdle are joined ventral to the vertebral column. In many reptiles—e.g. Lacerta—the ilium is directed backwards to unite with the sacrum, whilst an ischiopubic foramen appears, partly separating the ischium from the pubis. This same foramen is represented in birds and mammals by the obturator foramen, whilst in birds the ilium is fused with the ischium, running parallel to it, except for a small ilio-sciatic foramen. In birds the two halves of the girdle do not reach the midventral line, so that no symphysis is formed, whilst in mammals the two pubes become united in the midventral line to constitute the pubic symphysis.

Limb-girdles, as well as limbs, have disappeared secondarily in some Gnathostomata. Examples of forms where this has occurred are afforded by the Gymnophiona and snakes, whilst the whales have completely lost their pelvic girdles.

Skull. The skull consists essentially of a box, the cranium, enclosing the brain. On to this become fused the nasal and auditory capsules, and the whole constitutes the neurocranium. The remainder of the skeleton of the head is the visceral skeleton, consisting of the supports of the visceral arches and jaws : this is the splanchnocranium. Primitively such a skull is cartilaginous, but later becomes, to a greater or less extent, replaced by bone, whilst dermal bones become plastered on to the surface. In any case this cartilaginous skull, or chondrocranium, forms the basis of the structure of the skull, even of higher forms, and may well therefore be described first.

The floor of the chondrocranium consists essentially of a pair of trabeculæ in front and a pair of parachordals continuous with them behind. From each parachordal arises an occipital arch, the two fusing in the mid-dorsal line. To the parachordal and occipital arch of either side is firmly attached an auditory capsule, though a fenestra metotica is left between the hind wall of the capsule and the occipital arch for the egress of nerves IX and X. Immediately in front of the auditory capsules arises a pair of pilæ antoticæ, and these extend dorsally as far as the orbital cartilage, which itself arises as a transverse fold to form the roof of the orbit.

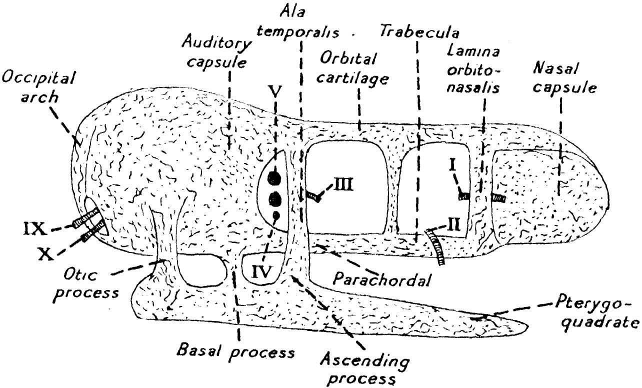


FIG. 177.—Diagram of chondrocranium.

A pair of pillars reaching from the trabeculæ to the orbital cartilages also contributes to the formation of the wall of the cranium. At the anterior end is a pair of nasal capsules. These are separated from each other by an internasal septum, formed from the trabeculæ, which here converge to the middle line and become fused, whilst posteriorly each is separated from the orbit by a lamina orbitonasalis between the orbital cartilage and the trabecula of its own side. Between the auditory capsule and the pila antotica emerge nerves V, VI and VII, whilst nerves III and IV pass in front of the pila antotica. Nerve II emerges behind the lamina orbitonasalis.

The skeleton of the jaws consists essentially of two almost parallel cartilages, the pterygo-quadrate comprising the upper jaw and the Meckel's cartilage the lower. The former is of great importance on account of its attachment to the neurocranium. There are typically three ways in which this may be effected. They are—

(A) *Amphistylic.* The pterygo-quadrate is here attached to the neurocranium both by the hyomandibula and by an otic process of its own abutting on to the auditory capsule. It is exemplified by a dogfish known as *Heptanchus.*

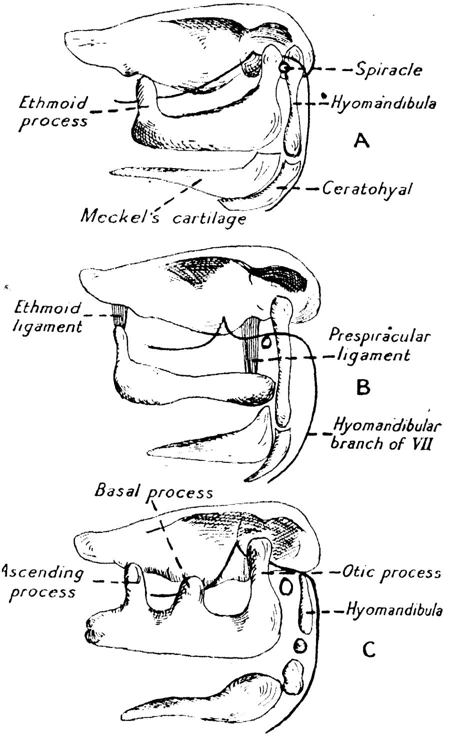


FIG. 178.—Diagrams to show jaw attachments.
A, Amphistylic. B, Hyostylic. C, Autostylic.

(B) *Hyostylic.* The pterygo-quadrate is completely free from the auditory capsule and is attached by the hyomandibula and by prespiracular and ethmoid ligaments. This condition obtains in *Scyllium.*

(C) *Autostylic.* In this type the hyomandibula plays no part in the suspension of the pterygo-quadrate, which has three processes of its own—the otic (posterior), basal and ascending (anterior). This is the condition found in Dipnoi and Tetrapoda. In consequence the hyomandibula is set free and forms the columella auris (stapes of mammals).

The jaws are formed typically from the skeleton of the first visceral arch, known as the mandibular and separating the mouth from the spiracle. There are further arches separating the gill-slits from each other. The second visceral arch lies immediately behind the spiracle, whilst there are five further arches, one behind each succeeding gill-slit. Each consists typically of four cartilages, named the pharyngobranchial (dorsal), epibranchial, ceratobranchial and hypobranchial. The pterygo-quadrate represents the epibranchial of its arch, and the Meckel's cartilage the ceratohyal. The skeleton of the second (hyoid) arch consists usually of an hyomandibula (epibranchial) and a ceratohyal (ceratobranchial), as in the dogfish.

The bony skull is formed from the chondrocranium partly by the ossification of cartilage already present and partly by the formation of dermal bones, which become plastered on to the surface immediately beneath the skin. The former are fairly constant throughout the Gnathostomata, but the latter vary in number and disposition. In primitive bony fish, Amphibia and reptiles this covering of dermal bones was more or less complete, except for vacuities for the eyes, pineal body and spiracles, the latter becoming the Eustachian tubes. Many of the bones may be identified in the Amphibia with those of the fish by the lateral-line canals which form grooves on their surfaces. Furthermore, the skull in Tetrapoda is movably articulated with the vertebral column by condyles. Of these there were primitively three, namely a pair of exoccipitals and a basioccipital. In higher forms either the exoccipitals or the basioccipital fall out of use in this respect, so that either one or two condyles remain. In reptiles and birds there is normally a single, median condyle, whilst in modern Amphibia and mammals there is a pair of exoccipitals. In reptiles, too, the covering of dermal bones was primitively complete, but no lateral-line canals remained. Later, however, this bony covering became perforated by fossæ. These are not to be confused with foramina, which actually penetrate to the brain-case: the fossæ perforate merely the superficial covering of dermal bones. Some of these fossæ persist in higher vertebrates, and the zygomatic arch forms the lower limit of the temporal fossa, bordered above by the parietal. In the higher Primates, including man, a downward extension of the parietal to the zygomatic arch completely closes off the orbit behind from the temporal fossa in front, whereas in other mammals the two are confluent. The brain of birds and mammals has become so much enlarged that certain membrane-bones now actually form part of the wall of the cranium, as exemplified by the alisphenoid and squamosal. In some reptiles and in mammals a false palate is formed by the inward extension of the maxillæ and palatines to the midventral line. The attachment of the jaws to the cranium has already been mentioned, and one of the cartilage-bones of the upper jaw—the quadrate—is important. This retains its otic process, which abuts against the auditory capsule. In certain reptiles it has become capable of movement independently of the squamosal and cranium. Thus the upper jaw can move relatively to the cranium and this condition, described as streptostylic, enables a wider gape than otherwise possible to be effected. This condition reaches its maximum development in snakes.

The lower jaw in the chondrocranium consists of but a single structure, namely Meckel's cartilage. The cartilage-bone formed by the ossification of this is the articular, and membrane-bones become plastered on to it. These are primitively numerous. In early Amphibia, for example, they consists of dentary, angular, supra-angular, splenial and coronoid bones. Normally the two halves of the lower jaw are firmly united in the middle line anteriorly, but in snakes they remain separate, thereby contributing further to the size of the gape. The evolution of the lower jaw in mammalian ancestors is interesting. It shows a progressive increase in the size of the dentary bone on either side, and a corresponding reduction in the remainder. Originally the articular of the lower jaw articulated with the quadrate of the neurocranium. But now the dentary comes to develop a vertical coronoid process, which later comes into contact with the squamosal, eventually affording the means of articulation of the lower jaw. This means that the quadrate and articular have now been set free from their original function, and the new dentary-squamosal articulation is completed before they undergo an interesting change in position. They become eventually intercalated between the tympanic membrane and the columella auris, so that, instead of the single one, a chain of three ear ossicles is now present. The columella auris, which fits against the membrane covering the fenestra ovalis, becomes known as the stapes, whilst the quadrate, situated next to the stapes, is called the incus. The articular becomes the malleus, and abuts on to the inner side of the tympanum. The majority of the remaining dermal bones of the lower jaw have disappeared completely in mammals, but the angular remains on either side to give rise to the tympanic bulla.

The remainder of the splanchnocranium is variously represented in the different classes of the Gnathostomata by the hyoid apparatus. In Amphibia it is formed mainly from the ceratohyals of the second visceral arch and the ventral elements of the first and second branchials. It is important in the forcing of air into the lungs for respiratory purposes. The structure of the hyoid is similar in reptiles. The hyoid in birds consists of the ceratohyal and the basihyal of the second (hyoid) visceral arch, together with the ceratobranchial and basibranchial elements of the first branchial arch. The mammalian hyoid is small, except for the posterior cornua, which represent the ceratobranchials of the first branchial arch. It is possible that the cartilages covering the larynx and trachea represent vestiges of other visceral arches. In all the Tetrapoda the hyomandibula has become represented by the columella auris (stapes of mammals).

SKIN

Skin covers the entire surface of the body, and functions principally for protection. It receives a copious supply of nerve-endings, and in places becomes especially adapted to the reception of stimuli. It gives rise also to a number of derivatives, including scales, feathers, teeth and hair, the origin of which will be described.

It consists essentially of a superficial epidermis of ectodermal origin, with a mesodermal dermis beneath. The structure of the skin in individual types has already been described, and it should be remembered that *Amphioxus* differs from the remainder of the Chordata in that its epidermis is but one cell thick. In Gnathostomata the epidermis is itself divisible into a Malpighian layer of actively-dividing cells next the dermis, and a superficial Keratin layer composed of horny scales. Apart from the derivatives to which it gives rise the skin itself may be variously modified. Thus the epidermis covering the cornea of the eye is very thin and transparent, forming the conjunctiva. The glands of the skin, exemplified by the sebaceous, sweat and mammary glands of mammals, are all formed by invagination of the epidermis into the dermis. Furthermore, the horny scales on the feet of birds and over the general body-surface of reptiles are epidermal structures. The dermis, too, is not without certain modifications. Thus the dermal bones arise from the dermis. The horns of cattle and the antlers of deer have a core of dermal bone produced in a similar manner. In connexion with the dermis definite muscles occur. Thus there are the erector pili muscles connected with the bases of the hair-follicles, whilst facial movements are accommodated by similar muscles. In some animals a panniculus carnosus muscle is developed in relation to the dermis of the trunk, enabling the animal to shake its skin.

Origin of Scales. A number of mesoderm cells becomes collected into a small group immediately beneath the epidermis. This latter becomes evaginated, and the layer of epidermis lining the evagination becomes an enamel organ. Meanwhile the mesoderm cells become arranged in the form of a cone, projecting into the evagination, and they commence to produce dentine on their outer side. This forms the main bulk of the scale, and over its surface the enamel organ secretes a cap of enamel. The base of the scale remains open, communicating with the cavity of the scale, known as the pulp-cavity. Eventually the structure breaks through the surface, and scales at the margin of the jaws constitute the biting teeth.

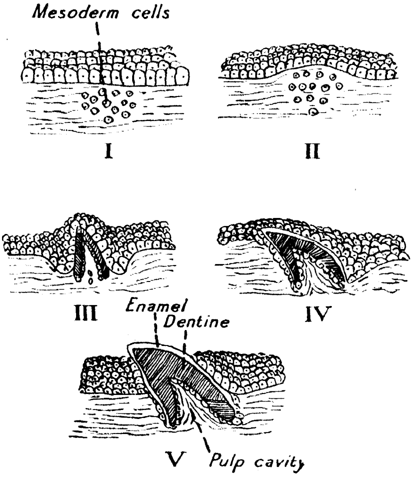


Fig. 179.—Development of denticle.

Origin of Teeth. The teeth of higher vertebrates resemble essentially the scales of the dogfish, though they arise in a somewhat different manner. A dental lamina is formed as a longitudinal invagination of the epidermis into the dermis around the margin of both jaws. At its base teeth appear. A fold arises on the outer side of the dental lamina, and this constitutes a tooth-germ. The innermost layer of the epidermis forms an enamel organ, whilst the cavity of the tooth-germ becomes filled with mesoderm cells, known as odontoblasts, which give rise to dentine. Connective tissue comes to surround the whole tooth-germ, thus forming a tooth-sac, whilst the cavity of the tooth-germ is now known as a dental papilla. Cement is formed on the outer surface of the tooth, and consists of true bone, containing bone corpuscles. A cap of enamel is secreted over the upper surface of the tooth by the enamel organ. In most teeth the supply of nourishment is cut off by the closure of the base. Occasionally, as in the incisor teeth of the rabbit, the roots remain open, so that the teeth continue to grow. In this condition they are described as having persistent palps.

Replacement of teeth is perpetual in the lower vertebrates, which are therefore said to be polyphyodont, in contradistinction to the diphyodont condition in mammals, where there are only two generations, namely a deciduous and a permanent. The members of the former set are pushed out as the permanent teeth approach the surface of the gums.

The various types of mammalian teeth have already been mentioned (page 187). In herbivorous forms the incisors are typically separated by a wide diastema from the premolars, whilst the crown of the grinding teeth is elongated and formed into deep valleys and high ridges, the valleys being filled with cement. Since enamel is harder than cement, and cement than dentine, a good grinding surface is retained throughout life. In carnivorous forms the canine teeth are typically well developed, whilst the last premolar in the upper jaw and the first molar in the lower jaw becomes specially enlarged to form the carnassial teeth. Primitively molar teeth possessed only three cusps or projections, but this simple condition has become secondarily modified to a great extent, whilst the roots of the molar teeth are also subdivided, forming fangs.

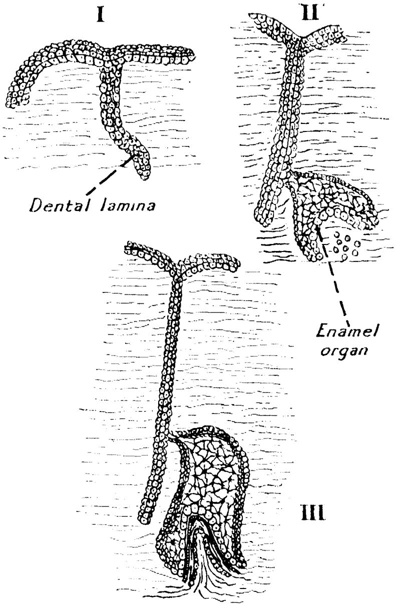


FIG. 180.—Vertical section through jaw, showing development of a tooth.

Origin of Feathers. The initial stages of the development of a feather are much like those of a scale, and it has been held that feathers have arisen evolutionarily by a process of fraying out of reptilian scales. Although scales and feathers are both epidermal products and of similar nature the bulk of available evidence would lead to the conclusion that feathers arose independently, although doubtless in close association with scales. There is little doubt that a layer of simple feathers as a warmth-retaining mechanism arose before birds had acquired powers of flight.

Feathers arise as a thickening of the epidermis, beneath which a concentration of connective tissue occurs. This rudiment gives rise to a papilla, projecting backwards, and becomes sunk into a depression, thus forming a feather-follicle. The stratum Malpighi becomes thickened, enclosed by the stratum corneum and surrounding a cone of dermis. The stratum Malpighi becomes divided into a series of columns surrounding the central pulp. These columns become cornified and are the future rami, by a splitting of which barbules are formed. The above type of development is characteristic of down-feathers, whilst in the formation of contour feathers the ramus rudiments run in a spiral course. Thus the feather has eventually to unroll and flatten out.

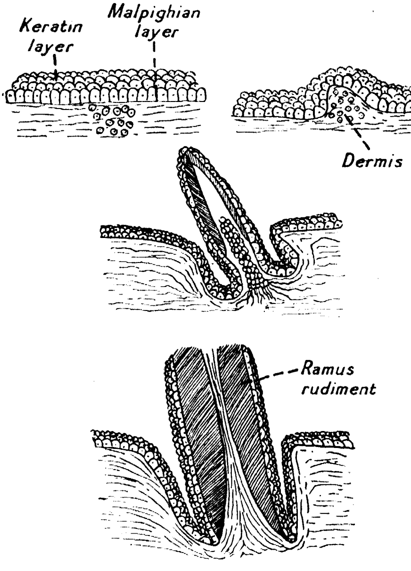


FIG. 181.—Development of feather.

Origin of Hair. There are typically two kinds of hair, namely a soft, under fur and a stiffer, outer covering. The former is especially well developed in animals living in cold climates. Tactile vibrissæ of the lips and the eye-lashes are modified hairs. In the formation of an hair the Malpighian layer becomes depressed, and at the base of this depression an hair-papilla is evaginated towards the surface of the body. Into this papilla extends mesodermal tissue, including blood-vessels. The stratum Malpighi becomes thickened over the papilla, and forms the growing surface of the hair. As the hair grows considerable differentiation occurs. Thus the hair comes to consist of a central medulla, containing numerous air-spaces and covered by a sheath, itself divisible into four layers, the innermost of which is deeply pigmented. Evagination of the epidermis lining the hair-follicle gives rise to sebaceous glands, which serve for lubrication.

The evolutionary origin of hairs is unknown, but it is certain that they were not derived directly from reptilian scales, since the latter start development by an outpushing of the epidermis, whereas hairs arise from an invagination of that layer. There is no intermediate condition known between hairs and scales.

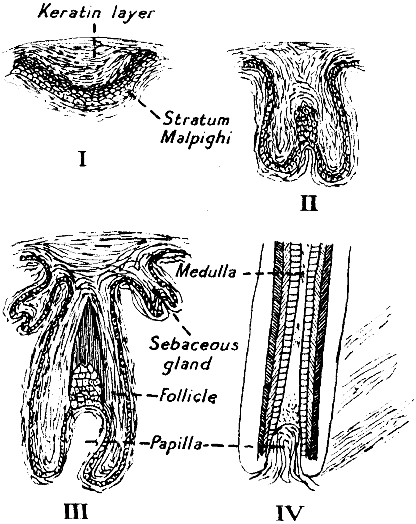


Fig. 182.—Development of a hair.

Functions of the Skin and its Derivatives. The skin itself serves for protection, excretion and the reception of stimuli from the outside world. In accordance with its protective function the outer layer is hardened, whilst in many forms scales are formed over the whole or parts of the body. Claws are epidermal structures of protective significance, whilst horns and antlers function for aggression. The skin bears also a number of glandular structures. These are of three sorts in mammals. The sebaceous glands produce an oily liquid for the lubrication of hairs, whilst the sweat glands extract water from neighbouring cells and blood-vessels and cast it on to the surface. The mammary glands, situated on the ventral surface of the trunk, produce a milky secretion for the nourishment of newly-born offspring. In the Amphibia the mucous glands are important on account of their keeping moist the surface of the body and thus assisting the respiratory process. Hairs and feathers function primitively for the prevention of the loss of heat from the body-surface, since they imprison a layer of air, which is notably a bad conductor of heat. Heat-regulation is effected also by the supply of blood to the capillaries of the dermis. When these dilate blood comes nearer to the surface, so that heat may be lost, whilst when they are contracted such loss of heat is prevented by retention of the blood farther within the body. The pouring of sweat on to the surface is also a means of keeping down body-temperature, for the latent heat of vaporisation must be derived from the body. Practically the only involuntary method of raising body-temperature is that of shivering. Feathers have become subsequently flattened and expanded to assist in flight, whilst the horn of the rhinoceros consists of fused hair and is a weapon of defence.

CHAPTER XXV

NUTRITION

NUTRITION is the sum-total of processes whereby raw materials are converted into body-substance. It is typically capable of subdivision into a number of stages. The first is the taking of food, possibly prefaced by its capture. The food thus taken is mostly insoluble. Before it can be absorbed into the body it has to be rendered both soluble and assimilable. This is the process of digestion. Merely to be soluble is often not sufficient. Thus, for example, ordinary sugar (sucrose) is soluble, but must be hydrolysed to form glucose and fructose before absorption through the internal mucosa (epithelium) can occur. This bringing of the food into an assimilable condition is effected by its treatment with a number of juices produced in the body. Following this absorption assimilation takes place, the molecules of the simple, soluble compounds recombining eventually to constitute body-substance. The process of digestion will first be considered from the point of view of the structures which accommodate it in the various groups of the animal kingdom.

Digestive Organs. In the Protozoa food is ingested—i.e. it is taken in over the body-surface, as in *Amœba*—and there is no specialised mouth or alimentary canal along which it may be passed. Instead it is circulated through the general cytoplasm of the organism, and this produces chemical substances which render the nutritious parts of the food soluble. The question of absorption, other than from the food-vacuoles, does not arise, so that it is possible that decomposition does not proceed so far as when the food has to be absorbed through a mucosa.

In the Cœlenterata a definite mouth and gastral cavity (enteron) exist, as shown in *Hydra* and *Obelia*. But the process of ingestion still occurs, though digestion probably accompanies it, for a certain amount of digestive material may well be produced to act on the food in the enteron.

Above the Cœlenterata the digestive system is typically the same throughout, except in degenerate forms, such as the parasitic Platyhelminthes. It consists essentially of a tube, or alimentary canal, through which passes the food. During its passage it is acted upon by a number of digestive juices, produced either by special digestive diverticula or by the lining of the gut. In the later part of the gut the soluble and assimilable part of the food is absorbed, whilst solid waste matter escapes through an aperture, usually termed an anus. In the parasitic forms, as exemplified by *Tænia*, a gut may be entirely absent, the liquid food in which the animal is bathed being absorbed over the entire body-surface. The individual characteristics of the alimentary canal in various groups has already been considered under the headings of the different types.

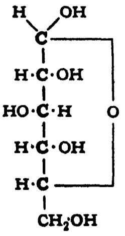
Foods. It is essential now, therefore, to consider something of the chemical nature of foods and of the changes which take place during digestion. For this purpose the digestive process in a typical mammal may be considered, most of which will be strictly applicable to man. There are six essential constituents of a satisfactory diet, classified according to their chemical constitution. They are

(*a*) Carbohydrates.
(*b*) Proteins.
(*c*) Fats.
(*d*) Vitamins.
(*e*) Mineral salts.
(*f*) Water.

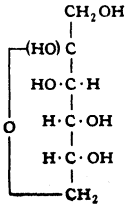
They will be considered individually.

(*a*) CARBOHYDRATES. Carbohydrates are compounds containing only carbon, hydrogen and oxygen, the numbers of hydrogen and oxygen atoms in a molecule being in the ratio of two to one. They are further subdivided into monosaccharides, disaccharides and polysaccharides.

(i) Monosaccharides have the general formula $C_nH_{2n}O_n$, where the value of n ranges from 2 to 10. By far the most important are the hexose sugars, of formula $C_6H_{12}O_6$. The two best known of these are glucose and fructose. Glucose occurs in fruit, in blood and other tissue-fluids of animals, and is an end-product of carbohydrate digestion. Fructose also occurs in fruits, and is an important constituent of honey. The formulæ of these two sugars are as follows—



Glucose



Fructose

Thus, with reagents strong enough to break the ring, glucose will react as an aldehyde and fructose as a ketone, and they differ from each other almost as an aldehyde differs from a ketone. Since they both contain a —CH_2OH group they are capable of acting as primary alcohols as well as secondary, the $>CH.OH$ group also being present.

(ii) Disaccharides are most commonly formed as a result of condensation between two molecules of an hexose monosaccharide—i.e. they combine with the elimination of water. Thus—

$$2C_6H_{12}O_6 \rightleftharpoons C_{12}H_{22}O_{11} + H_2O.$$

If they retain the aldehydic or ketonic groups they behave somewhat similarly to the monosaccharides. The two most important of those having these properties are maltose and lactose. Maltose occurs in malt and is formed by the hydrolysis of starch or glycogen, whereas lactose is the sugar of milk, and is readily converted by bacterial action into lactic acid, as when milk goes sour. On hydrolysis maltose yields glucose and galactose, whilst lactose produces only glucose.

(iii) Polysaccharides have the general formula $(C_6H_{10}O_5)_n$, where n is of such a value that molecular weights range from 1,600 to 30,000. They occur commonly in plants, the best known forms of which are starch, cellulose and inulin, whilst the glycogen of animals belongs to the same class. On hydrolysis they eventually produce monosaccharides.

Chemical Tests for Carbohydrates

(*a*) Carbohydrates. To a small quantity of the solution add a few drops of 3% thymol and an excess of concentrated hydrochloric acid. Boiling for a few minutes with repeated shaking will result in the appearance of a carmine coloration if a carbohydrate is present. The test is satisfactory even for carbohydrates insoluble in water, since they dissolve in the hydrochloric acid.

(*b*) Sugars only. (i) To a small quantity of the solution add about 3 c.c. of concentrated nitric acid and a few drops of dilute potassium chromate solution. A blue coloration soon appears if a sugar is present.

(ii) If a small quantity of sodium hydroxide solution be added to a solution containing a reducing sugar and the whole warmed, a brown coloration results.

(iii) Trommer's test. Two drops of a dilute solution of copper sulphate are added to a small quantity of a solution of a reducing sugar. To this sufficient caustic soda is added to redissolve the precipitate of copper hydroxide formed. On gentle warming an orange-red precipitate of cuprous oxide is formed.

(iv) Fehling's test. If a solution of a reducing sugar be added to an equal volume of Fehling's solution and the whole boiled an orange-red precipitate of cuprous oxide is formed.

(v) Benedict's test. This will detect the presence of very small quantities of a reducing sugar. Some six drops of Benedict's solution are added to a small quantity of the solution of the reducing sugar and the whole is boiled for a short time. On cooling a yellow precipitate indicates the presence of a reducing sugar.

Benedict's solution—Dissolve 17·3 gms. of crystalline copper sulphate, 173 gms. of sodium citrate and 100 gms. of anhydrous sodium carbonate in 1 litre of water.

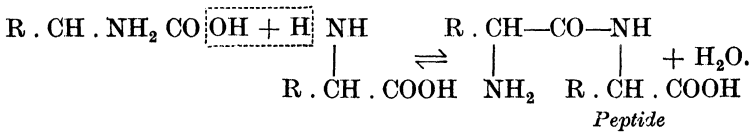
(vi) To an alkaline solution of a reducing sugar add a few drops of methylene blue. On boiling the blue colour gradually disappears.

(vii) To an ammoniacal solution of silver nitrate add a solution of the reducing sugar. On gently warming a silver mirror is formed on the sides of the test-tube.

Sugars other than reducing sugars may be made to respond to these tests if they are first hydrolysed by boiling with hydrochloric acid and the resultant solution then neutralised with caustic soda solution. In this way a reducing sugar may be distinguished from one of the non-reducing variety.

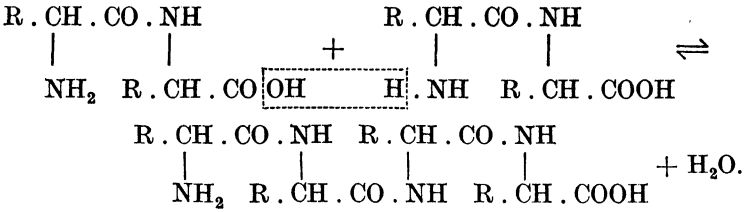
Finally, starch may be distinguished from cellulose by the addition of dilute iodine solution. Whereas starch gives a purple coloration cellulose, though at first showing blue, later turns brown.

(*b*) PROTEINS. Proteins are complex chemical substances occurring naturally and formed by condensation of amino-acids. They all contain carbon, hydrogen, oxygen and nitrogen, as well as possibly sulphur and phosphorus. The chemical structure of proteins may best be appreciated by a consideration of their formation from the simplest of their derivatives—an amino-acid. This is the amino-derivative of a fatty acid, and may be given the general formula $\mathrm{R\,.\,CH\,.\,NH_2\,.\,COOH}$. Two of these may condense together, resulting in the formation of a peptide, as shown.



$$\mathrm{R\,.\,CH\,.\,NH_2\,CO}\boxed{\mathrm{OH + H}}\begin{array}{c}\mathrm{NH}\\ |\\ \mathrm{R\,.\,CH\,.\,COOH}\end{array} \rightleftharpoons \underset{\textit{Peptide}}{\begin{array}{c}\mathrm{R\,.\,CH}\\ |\\ \mathrm{NH_2}\end{array}\mathrm{—CO—}\begin{array}{c}\mathrm{NH}\\ |\\ \mathrm{R\,.\,CH\,.\,COOH}\end{array}} + \mathrm{H_2O}.$$

Further condensation between two or more peptide molecules will result in the formation of a protein.



$$\begin{array}{llll} \mathrm{R.CH.CO.NH} & & \mathrm{R.CH.CO.NH} & \\ \;\; | \qquad\qquad\; | & + & \;\; | \qquad\qquad\; | & \rightleftharpoons \\ \mathrm{NH_2\;\; R.CH.CO}\boxed{\mathrm{OH} \qquad\quad \mathrm{H}} & & \mathrm{.NH\;\; R.CH.COOH} & \end{array}$$

$$\begin{array}{l} \mathrm{R.CH.CO.NH\;\; R.CH.CO.NH} \\ \;\; | \qquad\qquad\; | \qquad\quad\; | \qquad\qquad\; | \\ \mathrm{NH_2\;\; R.CH.CO.NH\;\; R.CH.COOH} \end{array} + H_2O.$$

A simple protein molecule

Thus on hydrolysis a protein is converted first to a peptide and then to an amino-acid.

Proteins are essential constituents of protoplasm, and for the purpose of the following chemical tests a protein solution may be conveniently made by shaking up egg albumen with twenty times its own volume of water, a little common salt being added.

Chemical Tests for Proteins

(i) The Biuret test. To some 5 c.c. of protein solution a little dilute caustic soda is first added. To this a few drops of very dilute copper sulphate solution (1%) are added, and the presence of a protein is indicated by a violet coloration.

(ii) The Arginine test. A small quantity of protein solution is made alkaline with caustic soda. Some five drops of 2% α-naphthol solution in alcohol and then some five drops of 2% sodium hypochlorite solution are added. An intense carmine coloration indicates the presence of a protein.

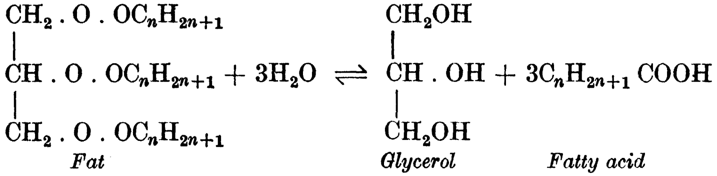
(iii) The Xantho-proteic test. A few drops of concentrated nitric acid are added to a small quantity of protein solution, and a white precipitate is first formed. On boiling this becomes yellow. If the solution is cooled and carefully made alkaline with ammonium hydroxide the yellow colour changes to orange.

(iv) Millon's test. Millon's reagent is obtained by dissolving 1 c.c. of mercury in 20 c.c. of concentrated nitric acid and diluting the whole with twice its volume of water. The action should be done in a fume cupboard and the acid added a few drops at a time.

When Millon's reagent is added to protein solution a white precipitate is first formed, and this changes to red on heating.

(v) Sulphur test. A few drops of lead acetate solution are added to the protein solution. Sufficient caustic soda is now added just to redissolve the precipitate of lead hydroxide which first forms. The mixture is now boiled, and the presence of sulphur is indicated by the formation of a dark brown solution, owing to the formation of lead sulphide.

(*c*) **Fats.** Fats are esters formed between the higher fatty acids and aliphatic alcohols. They contain, therefore, only carbon, hydrogen and oxygen, and are known as lipides, in contrast to the lipoids, which are closely allied to them but which are not in the form of esters. The commonest fats are the esters formed between glycerol and the higher fatty acids, of general formula $C_nH_{2n+1}COOH$. Thus the general formula for a fat may be represented as below, the equation showing the results of hydrolysis of such a fat:



$$\begin{array}{llll} CH_2 . O . OC_nH_{2n+1} & & CH_2OH & \\ | & & | & \\ CH . O . OC_nH_{2n+1} + 3H_2O & \rightleftharpoons & CH . OH + 3C_nH_{2n+1}\,COOH & \\ | & & | & \\ CH_2 . O . OC_nH_{2n+1} & & CH_2OH & \\ \quad\textit{Fat} & & \textit{Glycerol} & \textit{Fatty acid} \end{array}$$

The most commonly occurring fats are palmitin and stearin, found in animal and vegetable tissues. Their formulæ may be derived from the above general formula by assigning to n the values 15 and 17 respectively. Certain unsaturated acids, of general formula $C_nH_{2n-1}COOH$, form fats with glycerine, and these fats are also widely distributed in animal and plant bodies. The commonest is olein, oleic acid having the molecular formula $C_{17}H_{33}COOH$. Structurally it may be represented as

$$CH_3 . (CH_2)_7CH = CH . (CH_2)_7COOH.$$

Oleic acid

Since it is a monobasic acid three molecules of it will condense with one molecule of glycerine, forming one molecule of olein.

Chemical Tests for Fats

(i) Saponification. This is the term applied to the process of hydrolysis of fats. A small quantity of olive oil is shaken up with an equal quantity of sodium hydroxide solution. The test-tube containing this mixture is immersed in a bath of boiling water for about half an hour. On removal it is found that the hydrolysis has proceeded to a considerable extent. Consequently the contents of the test-tube separate out into three layers. At the bottom of the test-tube is unchanged alkali and the liberated glycerol. Above this there is formed on cooling a solid residue of the sodium salt of the fatty acid liberated, and this is a soap. Floating on the surface is unchanged oil. The contents are now carefully removed into separate tubes so that they may be tested.

The soap is first washed with water and then boiled with water until it dissolves. A few drops of hydrochloric acid are then added and the fatty acid is liberated as a white precipitate.

To the suspected glycerol a few drops of 5% potassium chromate solution are added, followed by an excess of nitric acid. The presence of glycerol causes the appearance of a blue coloration.

(*d*) Vitamins. Vitamins are essential in minute quantities to at any rate the higher animals, possibly for life and certainly for the maintenance of an healthy condition. They occur in the living tissues of animals and plants, and have been isolated, and in some cases synthesised. They are divisible into two classes, namely fat-soluble and water-soluble, according to the medium which serves as a solvent for them. They will be briefly described individually.

(i) Vitamin A is a fat-soluble compound and occurs in the oils of liver, cream and butter, in egg-yolk, seeds and green vegetables. It is formed only in plants, but may be stored in animals. In chemical form it is an unsaturated hydrocarbon, and can withstand considerable heating. Its deficiency appears to have two quite unrelated effects. In the young animal it causes faulty growth, whilst in the adult it brings about a cornification of certain of the more delicate epithelia. Thus ulcers frequently appear on the cornea, and in the alimentary and respiratory tracts.

(ii) Vitamin B consists of a group of substances, and in consequence is often referred to as vitamin B complex. It is water-soluble, and is very widely distributed in most natural foods. A chemical formula $C_{12}H_{17}N_3OS$ has been calculated for it by Windaus, who isolated it from yeast. In accordance with the view that vitamin B is a complex of substances a number of maladies may result from its deficiency. Of these the best known is the disease beri-beri, found in Eastern communities where the diet consists of "polished" rice. The "polishing" process results in the removal of the outer coat of the grains, where presumably the vitamin B appears. Birds fed on "polished" rice suffer so acutely from neuritis that they are eventually unable to stand. Other effects of vitamin B deficiency are dermatitis (inflammation of the skin), failure of growth, and a disease known as pellagra, confined to Italy and the U.S.A. and characterised by digestive disorders, dermatitis and possibly paralysis.

(iii) Vitamin C is water-soluble. It occurs in almost all fresh fruits and vegetables. It can withstand heat in the absence of oxygen, but is unstable in alkaline solution. Soda should therefore not be added to water in which vegetables are boiled. It is believed from the researches of Szent-Gyorgyi that vitamin C exists in two forms in tautomeric equilibrium—

$$HOOC\,.\,CO\,.\,C(OH) : CH\,.\,CH(OH)\,.\,CH_2OH \rightleftharpoons$$

Deficiency in vitamin C brings about scurvy. In infants this results in retarded growth and anæmia sets in, followed by the same symptoms as in the adult, namely soreness and bleeding of the gums and bleeding beneath the skin.

(iv) Vitamin D is fat-soluble. In distribution it resembles vitamin A, which it normally accompanies. It is formed from a precursor, known as ergosterol, by subjection to ultra-violet light, thus accounting for the significance of the exposure of the body to sunlight. Unlike vitamin A, vitamin D can be elaborated by animals if ergosterol is already present in the tissues. Ergosterol and vitamin D are isomeric, both having the molecular formula $C_{27}H_{42}O$. The importance of vitamin D is the regulation of calcium and phosphate metabolism. Thus deficiency in it is the cause of rickets, characterised by the defective ossification of a growing skeleton. Subnormal amounts of calcium and phosphate ions are absorbed from the intestine, whilst the amounts excreted with the urine are increased.

(v) Vitamin E is fat-soluble. It occurs chiefly in seeds, green vegetables and muscular tissues of animals. Its absence is supposed to bring about sexual sterility in the male, whereas in the female it causes the growth of the fœtus to be retarded, so that it dies before birth. (See also page 65.)

(*e*) MINERAL SALTS. Mineral salts are an essential constituent of the animal body. A remarkable fact was elucidated in the early part of the present century, namely that the concentration of salts in the plasma of the blood of vertebrates, and of invertebrates with a closed vascular system, closely resembled that of sea-water diluted to one-third its usual concentration. It is presumed that this is on account of their evolution from forms whose body-fluids were practically in open contact with the sea, and that when these ancestors lived the concentration of salts in the sea was only one-third of its present value. There is no doubt that certain ions play an important *rôle* in the regulation of the animal organism, the chief ones being hydrogen, carbonate, phosphate, calcium, magnesium, sodium, potassium, iron, sulphate, chloride and iodide. Their significance and occurrence may best be summarised in the form of a table (see page 291).

(*f*) WATER. Water is the chief quantitative constituent of living matter. The weight of water in a living organism varies from 60% to 95% of the total. It may be either free, acting merely as a solvent, or bound, in which case it is combined with tissue colloids. Water serves a number of purposes in the animal body. It forms the bulk of the structure, rendering the organism plastic but incompressible. It serves as a solvent, as well as

Ion	Form in which Absorbed	Function
Hydrogen	Water and acid salts	Essential constituent of water and organic foods. H ion concentration regulates heart-beat, respiration and enzymes
Carbonate	Acid Na and Ca carbonates	Regulation of H ion concentration
Phosphate	Acid Ca and Mg phosphate	Regulation of H ion concentration. Hardening of bones
Calcium	Acid phosphate and carbonate	Regulation of nerve-conductivity and muscular contraction. Coagulation of blood. Hardening of bones
Magnesium	Acid phosphate	Hardening of bones. Reverse effect of Ca on nerve-conductivity and muscular contraction
Sodium	Chloride and acid phosphate	Reduces muscular contraction
Potassium	Phosphate	Controls tissue-excitability and growth
Iron	Organic form	Constituent of hæmoglobin
Sulphur	Sulphates	Frequent constituent of protein
Chloride	Sodium chloride	Controls osmosis. Constituent of hydrochloric acid of stomach
Iodide	Iodides	Constituent of thyroxin

accommodating the assimilation of foods, for all reactions involved in this process take place in aqueous solution. Waste products are conveyed to the exterior in aqueous solution. Water also plays an important part in the regulation of body-temperature. Since it has so high a specific heat a great deal of heat must be lost before the temperature of the body falls appreciably, whilst when water is evaporated at the surface very efficient cooling occurs, since the latent heat of vaporisation is so high. Water is also of significance on account of the fact that waste carbon dioxide dissolves in it to form carbonic acid. From this hydrogen ions are set free. Thus when muscular activity is increased there is a corresponding rise in the output of carbon dioxide, and hence in the concentration of hydrogen ions. Accordingly both heart-beat and respiration are increased in rate.

Enzymes. Enzymes have already been referred to on account of their significance in the digestive process. At this point a few generalisations may be made about their properties. An enzyme is a biological catalyst which occurs in the body in a soluble, though colloidal, state. It is biological in the sense that it is produced only in a living organism, whilst its molecules are too large to pass through a parchment membrane. It is a catalyst in that it is produced only in small quantities; and is not used up during the reactions which it assists. In addition it has certain other characteristic properties.

Enzymes are highly specific in their action, which is to say that each will catalyse only one very definite reaction. In short it will react only with one type of substance and invariably yield the same product or products. Metallic catalysts, on the other hand, may be used to hasten many unrelated inorganic, or even organic, reactions.

Enzymes are highly sensitive to temperature-change, being completely inactivated by a few minutes' boiling. Every enzyme has an optimum temperature, though this may alter with variations in other conditions.

Hydrogen ion concentration has a marked effect on the action of enzymes. There are optimum values characteristic of each enzyme, whilst outside certain quite narrow limits the enzyme becomes totally inactivated. Ions other than those of hydrogen also control the activity of enzymes. For example, it is believed that amylase is unable to attack starch unless chloride ions are present, whilst ions of the heavy metals inhibit enzyme action.

Finally, it may be noticed that enzymes are classified according to the group of substances whose decomposition they accelerate. Previously they have been grouped according to the region of the

Class	Enzyme	Digestive Juice	Substance Acted Upon	End-product
A	Ptyalin	Saliva	Starch	Maltose
			Glycogen	Maltose
	Amylase	Pancreatic juice	Starch	Maltose
			Glycogen	Maltose
B	Maltase	Saliva and pancreatic juice	Maltose	Glucose
	Sucrase	Intestinal juice	Sucrose	Glucose and fructose
	Lactase	Intestinal juice	Lactose	Glucose and gallactose
C	Pepsin	Gastric juice	Proteins	Peptides
	Rennin	Gastric juice	Caseinogen	Casein
	Trypsin	Pancreatic juice	Proteins	Peptides
D	Erepsin	Pancreatic and intestinal juice	Peptides	Amino-acids
E	Lipase	Gastric and pancreatic juice	Fats	Fatty acids and alcohol

gut where they occurred. The digestive enzymes may be divided into classes, namely—

A. Polysaccharidases.	Conversion of polysaccharides to mono- and di-saccharides.
B. Saccharidases.	Conversion of disaccharides to monosaccharides.
C. Proteinases.	Conversion of proteins to peptides.
D. Aminases.	Conversion of peptides to amino-acids.
E. Estereases.	Conversion of fats to fatty acids and alcohol.

In the table on page 292 the various enzymes referred to in the previous descriptions of the processes of digestion in the frog and rabbit are arranged according to this functional classification.

CHAPTER XXVI

RESPIRATION AND OTHER FUNCTIONS OF THE BLOOD

THE whole animal organism is a mass of chemical reactions taking place continuously. These are sharply divisible into two classes. There are those concerned with the building up of body-material—i.e. they constitute the process of assimilation. The sum total of all such reactions is termed **anabolism.** As a result of this anabolism complex compounds are synthesised from simpler ones. This will necessarily involve the absorption of energy, such energy being converted into the potential energy of the chemical molecules. When work has to be performed by the organism this energy must be liberated, and thus transformed into kinetic energy. This is effected principally by means of respiration, usually involving direct oxidation of body-substance, though occasionally taking place in the absence of air, as mentioned later in the present chapter. The breaking down of complex chemical compounds, accompanied by the liberation of energy, is known as **katabolism.** Being essentially an oxidation process respiration is accompanied by an evolution of carbon dioxide. Thus anabolism and katabolism must be compensatory processes, the animal utilising its food in effecting the former, whilst respiration provides almost the only means whereby energy may be liberated. The two processes, anabolism and katabolism, together constitute **metabolism**. Metabolism may thus be defined as the sum total of chemical changes occurring within the organism. It is with the katabolic phase of metabolism that this chapter is principally concerned.

Respiratory Organs. An animal of small dimensions has no need of a system of channels for the carriage of oxygen about the body. Gaseous exchange takes place at the surface, oxygen being absorbed and carbon dioxide being evolved. Such animals, except such as are parasitic, live exclusively in water, so that they are dependent on the oxygen dissolved in their medium. Members of the phyla Protozoa, Cœlenterata and Platyhelminthes afford good instances of animals with no special respiratory organs.

In forms above the Platyhelminthes mere surface absorption of gases is inadequate to supply the respiratory needs. It may be that the skin acts for the absorption of oxygen, but once absorbed this oxygen is carried about the body in the blood, with the exception of the Echinoderma, where the fluid of the pseudhæmal system fulfils this purpose, and of the Insecta, discussed later. Thus in the earthworm absorption takes place through the skin, but the blood thus oxygenated is circulated throughout the body.

But certain modifications in structure of forms above the Annelida render this surface absorption inadequate. Thus the Arthropoda develop a skeleton of calcified chitin, whilst the body of the Mollusca is typically covered by a shell. Added to this the size of the body increases so much that the surface is no longer sufficient to accommodate gaseous exchange at the necessary rate. Accordingly special organs come to be set aside for this purpose. The crucial feature of all of them is the extent of their surface. They are constituted for the most part of very thin and highly-vascularised epithelium, so that the blood is brought into the closest possible contact with the air. Thus in the majority of aquatic arthropods gills are present. These take the form of branched filaments, copiously supplied with blood, and with a constant stream of water flowing over them. For this purpose they are usually contained in a chamber, as exemplified by *Astacus*. Terrestrial arthropods (not Insecta) have somewhat similar structures of a stiffer nature adapted for respiration in air. The lung-books of the spider afford an example of this. In the Mollusca the mantle is constituted by a fold of delicate skin, and serves to bring the blood into close contact with the air. In aquatic forms this mantle may be modified to form gills, as in *Anodonta.*

In the Chordata the same mechanism has been still further adapted to ensure satisfactory gaseous exchange. Thus not only are respiratory organs present, but the stream of the medium containing oxygen is more highly organised. In the lower forms gills are employed in adaptation to an aquatic mode of life. But a constant stream of water enters by the mouth (spiracles of some forms) and is passed to the exterior through the gill-slits, the walls of the gill-arches being highly vascularised and much subdivided.

In all the Tetrapoda lungs are the respiratory organs, and a special mechanism is developed for filling and emptying them of air at regular and very frequent intervals. Thus in the Amphibia air is forced from the mouth into a pair of lungs, each of which is a dilated sac with a large blood-supply to its walls. When the pressure on the air is released the waste air escapes to the exterior. Since Amphibia are in part aquatic the skin retains an important respiratory function, as in the frog. Being kept moist by a secretion of mucus it probably contributes a good deal to the respiratory mechanism even on land. In reptiles the system of respiratory organs does not differ essentially from that in Amphibia.

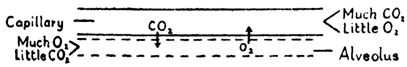
In birds respiration is an exceedingly important process, for flight makes an enormous demand on their energy supply. Accordingly there extend from the lungs air-spaces. These serve partly to render the animal lighter, but more importantly they avoid the existence of blind endings to the tubules of the lungs. Air passes right through the lungs to the air sacs at inspiration, whilst at expiration it is equally efficiently discharged. The actively muscular process in birds is expiration, whilst in mammals it is inspiration.

Mammalian respiration is similar in principle to that of the other Tetrapoda, but the filling and the emptying of the lungs are largely accommodated by the presence of a muscular diaphragm. An enormous amount of subdivision of the air-tubes occurs, so much so that the internal surface of the lungs in man is some thirty times the area of the body-surface.

Insects afford an important exception to the general rule that oxygen is absorbed into the blood at some specialised surface, for, as already indicated in Chapter VIII, air is conveyed direct to the tissues by a system of branching tubules, known as tracheæ and opening on to the body-surface by stigmata between the segments. Accordingly it is found that the blood-system of insects is poorly developed.

External and Internal Respiration. It will be evident, therefore, that in those organisms which distribute their oxygen by means of the blood respiration is divisible into two phases. Gaseous exchange occurs on two separate occasions, namely at the lungs or other respiratory surface, where oxygen is absorbed and carbon dioxide is eliminated, and in the tissues, where a similar process occurs. The former is termed the external phase of respiration and the latter the internal.

(*a*) External Respiration. As an example this process in a mammal will be considered. Air is drawn into the lungs by the expansion of the thoracic cavity. Within the lungs the walls of the blood-vessels and of the alveoli are so thin that, whilst not permitting blood to escape, gaseous exchange is possible. Thus in the air there is an high concentration (20%) of oxygen, whilst the proportion of carbon dioxide is low (0·02%). But in the impure blood, carried to the lungs along the pulmonary arteries, the reverse condition obtains. Accordingly diffusion occurs, oxygen passing from the alveoli into the capillaries of the blood-vessels and carbon dioxide in the reverse direction. This state of affairs may be represented diagrammatically by the following sketch:



A state of equilibrium is never attained, since the supply both of blood and of air is being constantly renewed.

(*b*) INTERNAL RESPIRATION. Oxygen thus absorbed into the blood is carried about the body until it reaches some organ requiring energy to do work. In such an organ the oxygen-content will be low, whilst a considerable quantity of carbon dioxide will be present. In consequence gaseous exchange, similar to that described as occurring in the lungs, takes place, oxygen being given up to the tissues and carbon dioxide carried away in the blood.

Chemistry of Respiration. It has previously been stated that oxygen is absorbed in the lungs by the blood. This is facilitated by the presence of the characteristic, red pigment of the blood, termed hæmoglobin. When this is brought into contact with oxygen it unites with it to form a loose compound, known as oxyhæmoglobin. This compound is therefore present in blood after its passage through the lungs, and is conveyed to necessitous tissues. In the absence of oxygen this compound readily dissociates, giving up its oxygen and being restored to its original form. This takes place in the tissues. Hæmoglobin itself is yellowish in colour, whilst oxyhæmoglobin is bright red. Hæmoglobin consists of a protein molecule (globin), together with an iron pigment, termed hæmatin ($C_{34}H_{32}N_4O_4FeOH$). This readily absorbs oxygen, and oxyhæmoglobin contains two displaceable atoms of oxygen per molecule. It might well be mentioned at this point that hæmoglobin forms a compound, known as carboxyhæmoglobin, in the presence of carbon monoxide. It is more stable than oxyhæmoglobin, and the CO group will replace the O present in this latter compound. Thus death due to carbon monoxide (the poisonous constituent of coal gas and exhaust fumes) is due to starvation of the tissues of oxygen, for the carboxyhæmoglobin is unable to take up oxygen to supply the tissues. In some of the lower invertebrates—e.g. Crustacea—hæmoglobin is replaced by hæmocyanin. This is a pigmented oxygen-carrier, similar to hæmoglobin but with the iron replaced by copper.

Carbon dioxide is carried away from the tissues in the plasma, uniting with the sodium carbonate present in that liquid to form the bicarbonate, according to the equation—

$$Na_2CO_3 + CO_2 + H_2O \rightleftharpoons 2NaHCO_3.$$

In the lungs this compound gives up its carbon dioxide, as in the reverse reaction.

The majority of compounds found in the animal body are not, if in the pure state, oxidised by exposure to atmospheric oxygen. Yet in the body they are readily oxidised. From this it is inferred that catalysts must be present, activating the substrate (material to be oxidised) and the oxygen. Catalysts effecting the former process are known as **dehydrases**, and the oxygen-activators are termed **oxidases.** The catalysts concerned in the oxidation process are sharply divided into two classes, namely those which are non-colloidal and can withstand the action of heat (they are described as being thermostable), and those which are colloidal and are destroyed by heat. Whilst both types are catalysts the latter only may be designated as enzymes. The chief oxidation catalysts are as follows.

(*a*) NON-COLLOIDAL CATALYSTS

(i) *Glutathione.* This is very widely distributed in animal tissues and occurs in two forms, the one readily oxidised and the other readily reduced. It is not certain how the oxidation takes place, but the reduction occurs when the catalyst brings about the oxidation of the substrate. Glutathione acts, therefore, as an oxygen-carrier.

(ii) *Cytochrome.* This resembles glutathione in its exceedingly wide distribution and its occurrence in two forms. Oxidation of cytochrome is brought about by atmospheric oxygen, whilst it is reduced when effecting the oxidation of the substrate. Like glutathione, therefore, it also acts as an oxygen-carrier.

(*b*) COLLOIDAL CATALYSTS (ENZYMES)

(i) *Dehydrases.* These activate the substrate to be oxidised, hydrogen atoms being rendered capable of ready transference to oxygen. They are highly specific—i.e. any one dehydrase will activate only a small class of chemical compounds. As a result of this activation and oxidation hydrogen peroxide is formed.

(ii) *Peroxidase.* This activates the hydrogen peroxide formed as stated above, and as a result a further portion of the substrate may be oxidised, whilst the hydrogen peroxide is reduced to water.

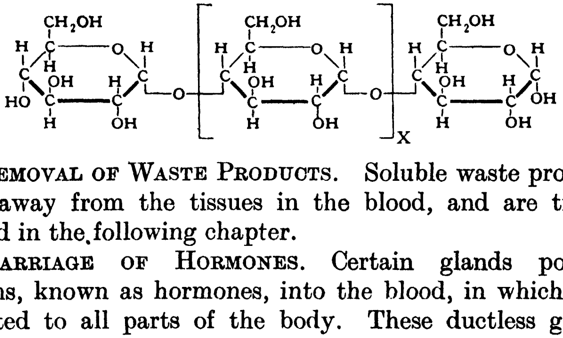
(iii) *Oxidase.* This catalyst (or group of catalysts) activates the oxygen to effect oxidation. It has been suggested that it does this by bringing about the reconversion of cytochrome to the oxidised form.

Anaerobic Respiration. Respiration occurs in some endoparasites in the absence of free oxygen: it is described as anaerobic. The substrates in such forms are activated by dehydrases and then they bring about the reduction of cytochrome. This in its turn is reoxidised by an oxidase.

FUNCTIONS OF BLOOD

As well as being so important as a carrier of oxygen and carbon dioxide the blood fulfils a number of other functions.

(i) CARRIAGE OF FOOD. Food rendered assimilable by the action of the digestive juices is absorbed either directly into a portal vein or into the lymphatic system. Even in the latter case it eventually reaches the blood, and is then distributed to various parts of the body. In this connexion it is important to notice that excess food can undergo temporary storage. Thus fatty substances are deposited in various parts of the body, whilst excess carbohydrate material is stored in the liver as glycogen. The formula for glycogen may be written



(ii) REMOVAL OF WASTE PRODUCTS. Soluble waste products are carried away from the tissues in the blood, and are treated as described in the following chapter.

(iii) CARRIAGE OF HORMONES. Certain glands pour their secretions, known as hormones, into the blood, in which they are distributed to all parts of the body. These ductless glands are described in Chapter XXIX.

(iv) TEMPORARY CLOSURE OF WOUNDS. When a wound is made, causing bleeding, it is rapidly closed over by the formation of a clot. This is due to the precipitation of a protein known as fibrin, formed by the union of fibrinogen with a small quantity of another protein, known as thrombin, under the influence of a quantity of oxygen far in excess of that to which the blood is accustomed. It is known that the presence of calcium salts in the blood-plasma is essential if clotting is to take place. After the clotting a clear liquid, termed the serum, remains. In this way loss of blood is prevented prior to the effecting of tissue-repair.

(v) PHAGOCYTOSIS. This involves the actual destruction of living matter by certain of the leucocytes (white blood-corpuscles) of the blood-stream. It normally takes the form of the engulfing of bacteria, but phagocytes may absorb unwanted tissue in the animal's own body. Thus the tail of the tadpole is absorbed during metamorphosis by the process of phagocytosis.

(vi) REGULATION OF BODY-TEMPERATURE. Since the blood is in constant circulation it tends to maintain all parts of the body at
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the same temperature. Since it contains a very high percentage of water it means that a lot of heat must be lost from the blood before the temperature falls to any appreciable extent. At the same time the body can be cooled by the dilation of capillaries in the skin so that the blood approaches nearer to the surface.

(vii) PRODUCTION OF ANTI-TOXINS. Most disease-causing (pathogenic) bacteria bring about their harmful effects by means of substances, known as toxins, which they secrete and which are carried about the body in the blood-stream. In an healthy animal the blood produces substances, known as anti-toxins, which neutralise the toxins and thus render them innocuous.

(viii) ERECTION OF THE PENIS. At copulation the penis becomes erected by the flowing into it of additional blood-supply, stimulated by the causes promoting the sexual act and returning to normal pressure on its completion.

CHAPTER XXVII

EXCRETION

As a result of the disrupting of the molecules of complex substances of which the body is made up simpler substances are formed, mostly in the nature of waste products. This consideration applies to both the liquid and the gaseous waste matter produced by the animal. Solid waste matter—i.e. fæces—is merely undigested food which has passed through the whole of the alimentary canal and resisted the action of the digestive enzymes. It is therefore not formed by the decomposition of more complex substances. The gaseous waste products of the animal body are carbon dioxide and water vapour. These are formed as a result of complete oxidation of the organic substances comprising the tissues. But protein waste matter must be of a different nature, since it often contains nitrogen. When proteins are partially decomposed their residue is carried away in the blood-stream and is eventually converted into the liquid waste matter eliminated by the animal. The process of excretion is the preparation for elimination of the liquid waste matter of the animal.

Excretory Organs. Throughout the whole animal kingdom it is found that specialised structures are present to deal with substances for excretion. Thus in the Protozoa contractile vacuoles exist. Within these liquid waste matter is collected, and when they reach a maximum size they contract, discharging their contents to the exterior. In *Amœba* there seems no fixed position for the contractile vacuole, as would be expected in view of this animal's continuously varying shape. In *Paramecium,* on the other hand, there are regularly found two contractile vacuoles, one anterior and one posterior, each contributed to by a number of formative vacuoles.

In the Cœlenterata the endoderm cells are copiously vacuolated, and possibly here the excretory products are collected. They are discharged into the enteron and voided through the mouth. There is less specialisation of excretory organs in this group than in any other.

In the Platyhelminthes the excretory organs take the form of long, branching tubules, ramifying through a considerable part of the tissues of the animal. The finest branches terminate in flame-cells (page 29). The excretory products are eventually shed by a pair of pores to the exterior.

The Annelida are characterised by the possession of well-developed excretory organs, termed nephridia, as seen in the earthworm. Their open ends project into the cœlom, developed in its true form for the first time in this group By ciliary currents the cœlomic fluid is passed through the coiled tube constituting each nephridium, each such tube taking the form of a number of hollow cells placed end to end. Finally the nephridium opens to the exterior. Waste products are first collected into the cells of the cœlomic epithelium of the intestinal region, constituting the chloragogenous tissue. When these cells disintegrate their products are shed into the cœlom and eliminated by the nephridia. A certain amount of waste matter probably escapes also through the dorsal pores.

In the Arthropoda a certain diversity of structure of excretory organs is encountered. Thus the insects typically possess a number of Malpighian tubules. These extend into the hæmocœl and absorb from it waste products, which are passed into the gut and discharged with the fæces. Like the excretory organs of Platyhelminthes and Annelida, they are of ectodermal origin, for they are formed by a series of evaginations from the anterior end of the proctodæum. In the crayfish, however, the excretory organs are a pair of sacs of mesodermal origin, and known therefore as cœlomoducts. From their characteristic colour they are known as the green glands, and each consists of a tube or duct, connected with a glandular vesicle below. This terminates in a blind end-sac, believed to enclose a portion of the cœlom.

In the Mollusca also the excretory organs are of mesodermal origin. They consist of a pair of tubes in communication with the pericardium, as already described. They are actually derived from the wall of the cœlom and establish communication with the exterior.

The excretory system is not well developed in the Echinoderma. A pair of sacs, known as rectal cæca, are given off from the gut near the anus, and they are possibly excretory. More important are the amœboid cells in the cœlomic fluid. These collect waste products and pass them to the exterior through the thin walls of the dermal gills.

Amphioxus is remarkable amongst the Chordata in that its excretory organs are nephridia. These are ectodermal in origin and are described on page 107.

The remainder of the Chordata possess mesodermal kidneys, by means of which excretion is effected. As has already been pointed out (page 249) the mesodermal tubules constituting the kidneys become much subdivided, and a larger number of Malpighian corpuscles is formed. Each of these consists of a glomerulus, itself a network of capillaries formed by an artery supplying blood to the structure and a vein carrying the cleansed blood away. Now it will be observed that in all other parts of the body wherever an artery is seen in dissection accompanied by a vein the latter is always considerably larger than the former. But in the case of the artery and the vein constituting a glomerulus there is little or no discrepancy in size. Consequently the vein is not able to carry away the fluid matter of the blood (in contrast to the blood-corpuscles) as rapidly as it is supplied. As a result some of this fluid escapes into the cavity of the Bowman's capsule and is absorbed by its wall. In this way nitrogenous waste matter, together with excess mineral salts and possibly sugar, is got rid of. The molecules of protein are too large to escape from the blood, whilst during the passage of the fluid along the tubules of the kidney a certain amount of water and other substances is resorbed. It is worthy of note in this respect that the urine of reptiles and birds is so highly concentrated that by the time it reaches the exterior it is in the form of a whitish, semi-solid substance.

In all the Chordata the urine is conveyed away from the kidneys in a pair of ducts. In fish and Amphibia this duct is the primitive Wolffian duct, whilst in the remainder of the Gnathostomata, since the functional kidney is a metanephros, the ducts are represented by new structures, termed ureters.

Chemistry of Excretion. In order to understand the chemistry of excretion it is essential to trace the fate of food materials from the time of absorption into the blood. The metabolism of these substances may therefore be considered under three heads, namely those of carbohydrates, fats and proteins.

(*a*) CARBOHYDRATES. Carbohydrates are absorbed as the monosaccharides, galactose most rapidly, then glucose, and finally fructose. Galactose and fructose become converted into glucose in the portal blood-stream. Some of the glucose is converted in the liver into glycogen, whilst the remainder is retained in circulation in the blood as the carbohydrate currency. This conversion of glucose to glycogen is stimulated by an high sugar-content of the blood and by insulin (Chapter XXIX), whilst the reverse process is accelerated by a low concentration of sugar in the blood, low temperature and adrenalin (Chapter XXIX). The concentration in the blood is kept more or less constant, however, for if it rises above a certain definite maximum, called the threshold value, it is excreted in the urine. In muscles, too, glucose is converted into glycogen. In a working muscle some of this glycogen is converted into lactic acid, about one-fifth of which is oxidised to carbon dioxide and water, whilst the remainder is reconverted to glycogen, partly in the muscle itself and partly in the liver, whither it has been carried in the blood-stream. Some of the waste carbohydrate material may reach the urine in the form of lactic acid, or of a lactate, the salt of the acid.

In conclusion it may be mentioned that one gramme of hexose sugar undergoing complete combustion to carbon dioxide and water liberates 4·19 kilocalories of heat.

(*b*) FATS. After absorption the derivatives of the fats, namely fatty acids and glycerine, are distributed in the lymphatic system, and to a lesser extent in the portal blood system. In the comparative absence of fats from the diet they may be built up from excess carbohydrate and protein material. It is believed that most fatty acid metabolism occurs in the liver. In general it takes the form of the oxidation of the hydrogen attached to the β-carbon atom—i.e. the one neighbouring that directly connected to the —COOH group. Thus, if butyric acid be taken as a simple example, acetoacetic acid is formed, as shown in the equation—

$$CH_3\overset{\beta}{CH_2}\overset{\alpha}{CH_2}COOH + 2O \rightarrow CH_3CO \,.\, CH_2COOH.$$

Butyric acid *Acetoacetic acid*

This may then become further oxidised, with the formation of acetic acid, water and carbon dioxide.

$$CH_3CO \,.\, CH_2COOH + 4O \rightarrow CH_3COOH + 2CO_2 + HO.$$

Acetoacetic acid *Acetic acid*

This is finally completely oxidised to carbon dioxide and water.

$$CH_3COOH + 4O \rightarrow 2CO_2 + 2H_2O.$$

Acetic acid

One gramme of a fatty acid on such complete combustion yields 9·4 kilocalories of heat.

As well as the above a little of the acetoacetic acid may behave differently. It may be—

(i) Reduced to β-hydroxybutyric acid, as in the equation

$$CH_3CO \,.\, CH_2COOH + 2H \rightarrow CH_3CH(OH)CH_2COOH.$$

Acetoacetic acid *β-hydroxybutyric acid*

or (ii) Converted into acetone, according to the equation

$$CH_3CO \,.\, CH_2COOH \rightarrow (CH_3)_2\,C = O + CO_2.$$

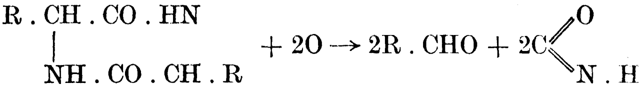
Acetoacetic acid *Acetone*

Thus, in such an example, the urine may contain small quantities of acetic acid, acetone and β-hydroxybutyric acid. But the presence of glucose appears to be essential to normal fatty acid metabolism. In its shortage the amounts of acetone and β-hydroxybutyric acid may be increased to as much as three hundred times the normal content.

(c) PROTEINS. Proteins enter the blood as amino-acids, of which there is always a large excess. Unlike fats and carbohydrates these acids cannot be stored by the animal, so that they must be eliminated. They are first of all de-aminated in the liver—i.e. their nitrogen content is removed and a fatty acid or its hydroxy-derivative remains. It was at one time held that this took place with the formation of ammonia, as, for example, suggested in the following equation—

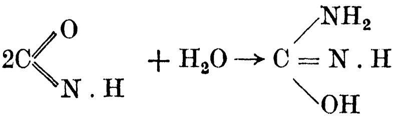
$$\underset{\textit{Amino-acid}}{\mathrm{R\,.\,CH(NH_2)COOH}} + \mathrm{2H} \rightarrow \underset{\textit{Fatty acid}}{\mathrm{R\,.\,CH_2\,.\,COOH}} + \mathrm{NH_3}.$$

But no free ammonia has ever been found in living tissues. It is believed rather that the amino-acids become united to form a cyclopeptide, as already described (page 286). This becomes oxidised to form an aldehyde derivative and cyanic acid. The latter immediately undergoes hydrolysis to produce urea, so that it is never identified in the living tissue. These reactions may be represented by the following equations—

(i) 

$$\begin{array}{l}\mathrm{R\,.\,CH\,.\,CO\,.\,HN}\\ \quad|\\ \mathrm{NH\,.\,CO\,.\,CH\,.\,R}\end{array} + \mathrm{2O} \rightarrow \mathrm{2R\,.\,CHO} + \mathrm{2C}\begin{array}{l}\nearrow \mathrm{O}\\ \searrow \mathrm{N\,.\,H}\end{array}$$

Cyclopeptide *Aldehyde* *Cyanic acid*

(ii) 

$$\mathrm{2C}\begin{array}{l}\nearrow \mathrm{O}\\ \searrow \mathrm{N\,.\,H}\end{array} + \mathrm{H_2O} \rightarrow \mathrm{C}\begin{array}{l}\nearrow \mathrm{NH_2}\\ = \mathrm{N\,.\,H}\\ \searrow \mathrm{OH}\end{array}$$

Cyanic acid *Urea*

These reactions are effected in the liver, and the urea-laden blood ultimately reaches the kidneys, where this compound is extracted in solution and conveyed to the exterior.

Other Constituents of Urine. As well as the compounds mentioned previously a number of other substances may be found in urine. Each will be dealt with briefly in turn.

(i) Ammonia. This is present in small quantities as ammonium chloride, phosphate and sulphate.

(ii) Sodium chloride. This occurs to the extent of about 1%. As with sugars there is a definite threshold value for this and all other salts. When the concentration of these salts in the blood surpasses this maximum the excess is eliminated by the kidneys and evacuated in the urine.

(iii) Potassium chloride. This occurs in a concentration lower than that of sodium chloride.

(iv) Phosphates of calcium, magnesium and potassium occur.

(v) Potassium and magnesium sulphate.

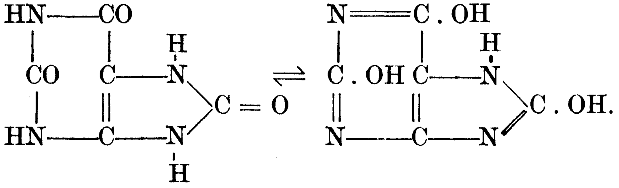
(vi) Hippuric acid is present in the urine of horses and other herbivores. It is benzoyl glycocoll, having the formula—

$$C_6H_5CO\,.\,NH\,.\,CH_2COOH.$$

Hippuric acid

(vii) Creatinine is liberated as a result of muscular activity and occurs in all mammalian urine.

(viii) Uric acid is found abundantly in the urine of reptiles and birds. It exists in two forms in tautomeric equilibrium—



A number of these products, especially urea and uric acid, have been identified in the excretory products of various Invertebrata.

CHAPTER XXVIII

REPRODUCTION

REPRODUCTION is the process whereby living organisms give rise to further individuals ultimately of the same bodily form. On the successful practice of reproduction depends the perpetuation of the race. A few points in the above definition may be considered a little more fully. Reproduction is the sole province of living matter: it is one of the diagnostic features of living matter. Reproduction may be effected by a single living organism, acting alone. In such a case the reproduction must be asexual (see later), or the organism must be self-fertilised. In other cases two organisms take part in the process of reproduction. In such a case the two essential counterparts must both contribute something to the new organism or organisms produced. Their exact contribution will be more fully understood when the process has been more fully discussed. It was stated in the definition that the organisms formed as a result of reproduction *ultimately* resemble their parents. They may not do so immediately. For example, reproduction in the frog results first in the formation of a tadpole. This larva leads an independent existence for some time before metamorphosing into an adult frog. This phenomenon is even more marked, for example, in *Obelia*. The polyp stage reproduces medusæ, differing at any rate superficially from the parent forms. These medusæ eventually give rise to the polyp stage by a further process of reproduction (page 23).

Asexual and Sexual Reproduction. Reproduction is essentially of one of two forms. An organism, or part thereof, may give rise to one or more daughter individuals without any fusion of cells occurring. This type of reproduction is described as asexual. It is clearly exemplified by *Amœba* and other Protozoa, where the parent organism becomes constricted into two halves, each of which gives rise to a daughter individual. A process to some extent comparable to this occurs in the Cœlenterata. *Hydra*, for example, reproduces by the formation of buds. These come to resemble the parent polyp, and are eventually separated from it. This latter type of asexual reproduction by budding is often distinguished from that found in the Protozoa by being described as vegetative, though in the literal sense of the word it is still asexual. The fundamental characteristic of asexual reproduction is that no fusion of cells occurs. It would appear to be a characteristic of living matter, but in the higher animals this power of reproduction by budding is almost entirely lost. In the Platyhelminthes and Annelida it is represented by an ability to regenerate lost parts. Thus, if an earthworm be cut into two equal parts the head end will regenerate a new tail, and possibly the tail end a new head. In some marine worms fragmentation occurs as a normal method of reproduction, each portion being able to effect regeneration and thus complete the formation of an entire individual. Similarly a starfish is able to regenerate a lost arm. In the Chordata the only remnant of this primitive property of asexual reproduction is the ability to heal wounds.

Sexual reproduction, on the other hand, always involves the fusion of two cells. These cells are known as germ-cells or gametes, and the body produced by their fusion is a zygote. The essential feature of the fusion of two gametes is the coalescence of their nuclei, often distinguished by the name pronuclei. In the Protozoa sexual reproduction may involve the fusion of two whole organisms, since they are non-cellular. This is discussed in the following paragraph. In higher organisms special cells are liberated from the bodies of the parents, and these cells are produced in definite organs, called gonads. This being so it will be seen later that an highly-important feature in the evolution of the process of reproduction is the perfecting of the mechanism for bringing together of the gametes from two individuals so that they may fuse to form a zygote. This has involved specialisation both of the germ-cells themselves and of the organisms elaborating them.

Sex in the Protozoa. By a careful selection of forms the way in which the Protozoa have become adapted to the requirements of sexual reproduction may be understood. For this purpose three types will be considered.

Copromonas is a flagellate Protozoön found in water frequented by frogs. It normally reproduces asexually, the entire organism splitting longitudinally into two halves, each of which grows to the size of the adult. But eventually a form of sexual reproduction occurs. This is effected by the total fusion of two organisms; whole nuclei also coalesce. In this way a zygote is formed, which either secretes a cyst around itself and undergoes a period of rest, or else recommences ordinary, asexual reproduction. There is no possible distinction between the two fusing cells, so that the gametes are identical. This condition is known as **isogamy.**

Heteromita is also a flagellate Protozoön, and a culture of it may be obtained by keeping an infusion of heads of cod. It, too, reproduces by binary fission—i.e. asexually—but sexual reproduction also occurs. In this process the two fusing cells are identical in structure, but it is important to notice that whilst one of the gametes is attached by a flagellum to the substratum, the other swims actively upon it. The zygote thus formed becomes encysted, and later liberates a number of minute, nucleate bodies, each of which grows into a new *Heteromita.* Thus, though there is no structural discrepancy between the two fusing cells, there is something of a physiological distinction between them in their behaviour at conjugation. The one remains attached, whilst the other is active. This foreshadows an important distinction existing between the gametes of higher forms, and is the earliest physiological differentiation of sex. Passivity is a characteristic of the female gamete and motility of that of the male.

Coccidium schubergi is a parasite found in the lining of the intestine of *Lithobius.* A single *Coccidium* lives within a cell of the intestinal epithelium. Asexual reproduction occurs, and the daughter individuals thus formed attack fresh epithelial cells. Eventually sexual reproduction takes place. To accommodate this individual *Coccidia* behave differently. One may absorb a large amount of reserve food and become a rounded ovum, or female gamete. Another divides many times to form within the epithelial cell a number of minute spermatozoa, or male gametes. The latter are almost naked nuclei, possessing two long flagella, and they swim actively about the body, eventually penetrating and fusing with an ovum. As a sperm approaches an ovum the latter puts out a small cone of attraction to meet it, this representing its last vestige of motility. Thus in *Coccidium schubergi* the differentiation of sex is complete. The male gametes are reduced to a minimum size and they are motile, whilst the female gametes are practically sessile and are laden with food material. This phenomenon of fusion of unequal gametes is known as **anisogamy.**

Sex in Other Invertebrata. In the Protozoa every time a new individual is formed by reproduction the parent form or forms lose their own individual existence. Thus when *Amœba* undergoes binary fission the two daughter cells are all that remain. Sexual reproduction in other Protozoa similarly results in the disappearance of the parents. But in higher Invertebrata special parts of the organism, known as gonads, are set aside for the elaboration of gametes. These gametes are invariably of two kinds, namely ova and spermatozoa : isogamy is unknown in animals other than the Protozoa. The gonads concerned with the production of ova are the ovaries, whilst spermatozoa are elaborated in the testes. The distinction into male and female gametes becomes extended to the organisms which produce them. Thus an entire organism is described as male or female. Though normally a single organism produces either eggs or spermatozoa, but not both, it is found in some groups that both types of gamete are formed in the same individual, described in consequence as an hermaphrodite. Even in such forms as these it is rare for an individual to utilise its own sperms to fertilise its own eggs—i.e. to undergo self-fertilisation. Cross-fertilisation—i.e. the fusion of the eggs with the spermatozoa of a separate individual—is the rule.

In the Cœlenterata the medusæ are normally either male or female, but the Platyhelminthes are hermaphrodite. This is no doubt in adaptation to a parasitic mode of life, where it may not always be possible for two individuals of opposite sexes to bring about mutual fusion of their germ-cells. Self-fertilisation is frequently encountered amongst members of this phylum. The Annelida, too, are characteristically hermaphrodite, possibly due to their evolutionary descent from forms related to and resembling the Platyhelminthes. But almost invariably cross-fertilisation is effected, taking the form of an interchange of spermatozoa, as in the earthworm. The sexes are separate in the Arthropoda, and a certain degree of sexual dimorphism is evident—i.e. the sexes become distinguishable by clearly-demarcated, external characters. Appendages become modified for the transference and reception of spermatozoa. In the Mollusca sexes are usually separate, as they are in the Echinoderma. Some Mollusca, however, possess what is known as an hermaphrodite gland, as found in the snail. This produces both eggs and spermatozoa, though in separate compartments, and these reach the exterior by separate channels, as already described (page 94). The snail is incapable of self-fertilisation.

Fertilisation of eggs may take place either external to the body of the mother or within it. External fertilisation is found in the Cœlenterata, Arthropoda and Echinoderma, whilst in the earthworm it takes place within the clitellum, modified to form a cocoon. In the Arthropoda sperms are usually passed to the female by the male and become attached near the openings of the oviduct, as described for *Astacus* (page 81).

In conclusion of this brief *résumé* of the sexual attributes of the Invertebrata the attention of the reader is redirected to the phenomenon of alternation of generations found in the Cœlenterata, and discussed on page 23.

Sex in the Chordata. In all the Chordata the sexes are separate, whilst in all the Gnathostomata sexual dimorphism is the general rule. Granted that the sexes are separate it remains to trace the evolution of the mechanism for bringing about the fusion of gametes of one sex with those of the other, and the correlation of this phenomenon with the care of young during and after development.

In the fish fertilisation is usually external. There is normally a return to a breeding-ground at certain seasons, and at these times eggs and sperms are shed into the water without recourse to pairing by the potential parents. This means an enormous wastage both of eggs and of spermatozoa, for only a very small proportion of eggs can be successfully fertilised. The extent of this wastage is forcibly suggested by the fact that a single female cod lays well over three million eggs in one breeding season. In exceptional forms, notably the dogfish and its allies, the pelvic fins become modified in the male to form copulatory appendages, whereby spermatozoa are introduced into the cloaca of the female. This enables internal fertilisation to occur, subsequent to which the eggs are surrounded by horny cases for protection during development.

In the Amphibia, represented by the frog, fertilisation is still external, but differs from that of the fish in that pairing occurs. Thus the chances of successful fertilisation of an egg are greatly enhanced. Both fish and Amphibia can breed only in water.

Reptiles are mostly oviparous, i.e. they lay eggs, which ultimately hatch out. Fertilisation is, however, internal, in adaptation to breeding on land. In birds the condition is much the same as in reptiles. Spermatozoa are injected into the body of the female by an evaginable penis in the male, and fertilisation occurs high in the oviduct. During the passage of the egg to the exterior a calcareous shell is secreted around it. After being laid it is almost invariably incubated by one of the parents, and after birth the fledglings are nourished by the mother, in some cases on her regurgitated food, and in others on material which she collects for them.

In the above groups of Gnathostomata the eggs produced are large, for they contain copious supplies of nourishment for the developing embryo.

In mammals an important advance has been made on conditions in lower forms. Not only is fertilisation internal, but the embryo is retained within the body of the mother during development. In this period of gestation, as it is called, the fœtus (embryo retained within the body) is nourished by the mother, for it is attached to the wall of the uterus by a placenta, along which liquid foods travel and waste matter is carried away. The actual blood-streams of mother and embryo are not continuous, so that the latter must form its own blood during development. Subsequent to birth the young are nourished by a milky secretion produced in the mammary glands of the mother. In the Marsupial group of mammals, exemplified by the kangaroo, the young are born at an early stage and complete their development within the marsupial pouch. Thus in the mammal it is found that the egg is reduced in size, the embryo having no need of a store of reserve yolk.

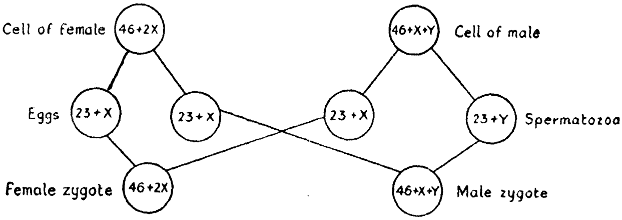
Breeding Season. In all the Gnathostomata except man breeding is a seasonal phenomenon. The effect of this on the organism can be judged by calling to mind the migratory flight of birds (page 211). Similar events occur in many fish. It is to be assumed that the cycle of events culminating in reproduction is initiated by climatic conditions, and the sequence of activities follows in regular succession, the completion of each stage providing the stimulus for the commencement of the next. The nervous mechanism responsible for the carrying out of the complicated series of reactions has already been discussed (pages 212 and 261).

In mammals the onset of the breeding season is characterised by fundamental changes in the reproductive organs of the female. Eggs are shed periodically from the ovaries, the phenomenon being termed ovulation. At the same time unfertilised eggs must be removed, whilst the epithelium of the genital tract must be kept fresh, so that fertilised eggs may readily effect attachment. Thus the old lining is periodically shed, carrying with it unfertilised eggs. This phenomenon is known as menstruation, and takes place only during the breeding season. The length of time between succeeding menstruations varies with different genera, but in man it is about twenty-eight days and takes place throughout the whole of the active sexual life of the female, except during pregnancy. It is to be assumed that the lack of a breeding season in man is a result of his ability to regulate his own environment. Seasonal changes can have obviously less effect, for, by varying the amount of clothes and artificial heat, he is able largely to counteract them. It is also part of a general evolutionary trend, for the breeding season in the Anthropoid apes is by no means so well marked as in lower mammals.

The sex instinct, or better the reproductive instinct, is fundamentally important to the perpetuation of the race. It is not essential for the existence of the individual that he or she should reproduce their kind. Accordingly it is found, particularly in mammals, where behaviour is to some extent arbitrary and is not so purely instinctive as in lower forms, that the act of copulation is made to provide intense pleasure to its participants, thereby ensuring to as great an extent as possible that the majority of individuals will complete it.

Determination of Sex. In conclusion there must be considered the mechanism whereby an individual is born either a male or a female. This is determined by the number of chromosomes (page

169) which the zygote contains. In mammals all the eggs produced by a given species will contain the same number of chromosomes. This will be the haploid number (page 169) for the species. Spermatozoa, on the other hand, are of two sorts, produced in equal numbers. One type contains exactly the same chromosome complement as does the egg, whilst the other contains either one less or one chromosome different in size and shape from any one in the egg. Suppose the diploid number of chromosomes is 48, as in man. Of these, 23 pairs are identical in male and female. It is the remaining two which are responsible for sex-determination. In the female this last pair consists of two identical X-chromosomes, whilst in the male they are unequal, one being known as the X-chromosome, since it resembles the same structures in the female, and its dissimilar counterpart as the Y-chromosome. Thus all the eggs formed in the female will contain 23 ordinary chromosomes (autosomes), plus one X-chromosome. Spermatozoa, on the other hand, contain a similar 23 autosomes, together with either an X-chromosome or a Y-chromosome. Thus when an egg is fertilised by a Y-containing spermatozoön the resultant zygote will develop into a male, whilst an X-containing spermatozoön will give rise to a female. These results may best be summarised by means of the following diagram.



CHAPTER XXIX

DUCTLESS GLANDS

In earlier chapters reference has frequently been made to structures known as ductless glands or endocrine organs. They are fundamentally important in the regulation of the activities of the animal body. They produce secretions, collectively known as **hormones**, and these are shed into the blood-stream instead of being conveyed away along ducts. Thus these hormones are capable of universal action throughout the body instead of exerting a mere local influence, as do the secretions of glands with ducts. It is probable that some of these endocrine organs have been developed during evolution from glands with ducts, whilst others have arisen from non-glandular structures. Some arise from two separate rudiments, which may even be derived from different germ-layers. In the following description the structure of the glands will first be considered, and reference to their evolutionary history will be made. Subsequently the functions of the hormones will be dealt with, together with a short account of the chemistry of the simpler ones. Except where otherwise stated it is to be assumed that the condition of the ductless glands in mammals is indicated in the description given.

Thyroid. The thyroid gland takes the form of a pair of pinkish lobes, situated one on either side of the anterior part of the trachea, the two lobes being united by a narrow, median lobe. It is enclosed in a thin, cartilaginous capsule, and is homologous with the endostyle of *Amphioxus*.

Pituitary. The pituitary is of double origin. It is formed from an ectodermal ingrowth from the roof of the mouth, known as the **hypophysis,** and of an **infundibulum,** taking the form of a downgrowth from the floor of the brain. The former appeared first in evolution, and is represented in *Amphioxus* by the wheel organ. In Tetrapoda this composite gland is divisible into four parts, known as the pars anterior, pars intermedia and pars tuberalis, all derived from the hypophysis, and the pars nervosa from the infundibulum.

Adrenal. This also is a composite organ. In the mammal it takes the form of a pair of small, rounded, yellowish bodies, situated one just anterior to either kidney. It consists of an external **cortex,** derived from cœlomic epithelium, and a central **medulla,** arising from nervous tissue. In the fish these components remain separate, the cortex being represented by an inter-renal body, and the medulla by a number of supra-renal bodies on or near the sympathetic nerve-cords. In all the Tetrapoda the elements have united, but in some cases the gland takes the form of transverse strips of tissue extending for some distance along the inner surface of the dorsal body-wall. This is so, for example, in the newt.

Thymus. This is a pale, soft, glandular mass of tissue, situated in the anterior part of the thorax. It is homologous with the tongue-bars of *Amphioxus*, and arises in fish as a series of paired downgrowths from the roof of the gill-slits.

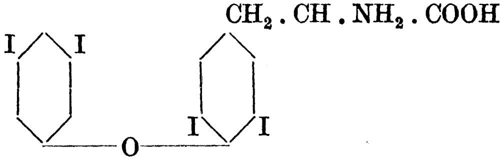
Pineal. In some lower forms, mostly extinct, this occurs as a median eye, but in higher vertebrates it loses this function and becomes glandular. It arises as a median, dorsal outgrowth from the diencephalon.

Parathyroid. This arises in all Tetrapoda from the floor of the third and fourth visceral clefts. The gland lies in close association with, or even embedded within, the thyroid.

Islets of Langerhans. These are microscopic islands of tissue situated in the pancreas and producing an hormone.

In addition to the above the ovaries, testes, small intestine and spleen also produce hormonic secretions.

Thyroxin. This is the hormone produced by the thyroid gland. It has been extracted and prepared in pure form, having the chemical constitution—



It functions to control the general metabolic rate, whilst in Amphibia it assists in the regulation of metamorphosis. Thyroidectomy (i.e. removal of the thyroid gland) in a tadpole does not check growth, but prevents metamorphosis, whilst if normal tadpoles are fed on thyroid extract metamorphosis is precocious. In presence of excess thyroxin the metabolic rate in man is increased, whilst nervous disorders and skin pigmentation occur. Shortage of thyroxin in the adult brings about myxœdema, resulting in the patient becoming fat, bald and sluggish. In the child the condition produced is known as cretinism, symptomised by general under-development. In cases of thyroxin deficiency administration of this substance by the mouth is possible, since it is not destroyed by the digestive juices. Goitre is the result of abnormal enlargement of the thyroid gland, often caused by lack of iodine in the diet. The gland becomes enlarged in an attempt to synthesise thyroxin from an inadequate supply of raw material.

Pituitary Hormones

(*a*) PHYONE. This is produced in the anterior part of the pituitary and stimulates the growth of bone. Lack of it results in infantilism and excess in gigantism. It can be administered only by injection.

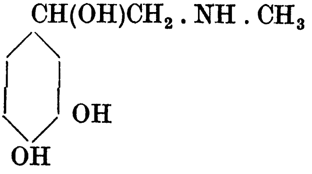
(*b*) SEX HORMONES. These are liberated from the anterior part of the pituitary and stimulate respectively the growth of the ovarian follicles and the corpora lutea.

(*c*) PITUITRIN. This is formed in the posterior lobe of the pituitary body and stimulates the contraction of unstriped muscle.

Adrenal Hormones

(*a*) CORTIN. This is the hormone, or mixture of hormones, produced in the cortex of the adrenal body. Its exact significance is not fully understood, but it is believed that it regulates metabolism and the growth and development of the female reproductive organs.

(*b*) ADRENALIN. This substance stimulates most structures supplied by the sympathetic nervous system. It brings about contraction of arterioles of the skin, whilst the rate and force of heart-beat are increased. Very importantly it brings about a raising of the concentration of sugar in the blood, for muscle glycogen is broken down and resynthesised in the liver, from which it can be liberated as glucose. Muscle glycogen does not act as a reserve, since it cannot be converted direct to glucose. Added to these properties adrenalin also regulates the contraction of miscellaneous muscles. It has been both extracted and synthesised, and has the chemical constitution—



Thymus Hormone. The thymus decreases in size with the advent of puberty, and little is known of its function. In birds it controls the formation of shell and shell-membranes of the eggs.

Parathyrin. This enzyme, produced in the parathyroid, controls the calcium metabolism of the organism. In presence of excess the increased concentration of the calcium ion in the blood brings about drowsiness, diarrhœa and increase in viscosity of the blood, so much so that circulation may fail. This increased concentration of calcium salts is due to none of them being eliminated in the urine, nor otherwise withdrawn from circulation—e.g. they are not used for the hardening of bones.

Insulin. Insulin is secreted by the islets of Langerhans. Its presence is necessary to promote the proper storage of carbohydrate material in the liver and muscles. In absence or deficiency of insulin the concentration of carbohydrate material in the blood falls very low, for most of it is excreted by the kidneys. This condition is known as diabetes and is treated by the injection of insulin extract.

Hormones of the Gonads. The ovaries and testes, as well as producing germ-cells, give rise to hormones responsible for the development of secondary sexual characters. That some at any rate of these hormones are present prior to puberty, or even to birth, is clearly indicated by the occasional production of a " free martin " amongst cattle. When twin cattle are born they develop normally if both of the same sex. But if of opposite sexes the male undergoes normal development, whilst the female becomes masculinised. This can be accounted for only on the assumption that the male hormone has been carried in the placental blood-stream to the female fœtus, where it has produced sexual disturbances. This hormone is probably different from the one liberated at puberty in the male to bring about the production of secondary sexual characters. Removal of the testes (castration) at an early stage prevents the appearance of these characters. Thus in mammals the male and female hormones differ qualitatively.

But in birds the position is somewhat remarkable. Whilst the comb and wattles seem to be controlled by the qualitative nature of the hormones of the two sexes, the plumage depends for its development on the gonads as physiological units and not as producers of hormones. The ovary is physiologically more expensive than the testes, and therefore the plumage is inferior in the female. That this is so has been forcibly demonstrated by a number of experiments involving gonadectomy and transplantation. Thus if the ovary be removed the plumage becomes that of a male, whilst castration of a male results, if anything, in the improvement of the plumage. Other transplantations are in keeping with these results, and most conclusive of all is the fact that implantation of additional testicular material into the male results in the plumage becoming female.

Hormones of the Corpus Luteum. When an egg is shed by the bursting of a Graafian follicle the torn tissues on the surface of the ovary become rapidly repaired if fertilisation does not occur. But if the egg is fertilised this region of the ovary becomes enlarged by rapid cell-division and invasion by connective tissue. In this way an endocrine organ is formed, known as the corpus luteum. The hormone produced by this gland has a number of functions. It inhibits œstrus (menstruation) and ovulation, it increases the sensitivity of the wall of the uterus, it maintains various conditions characteristic of pregnancy and stimulates the secretion of milk by the mammary glands.

Hormones of Small Intestine. When the acidified food passes from the stomach to the duodenum the walls of the latter become stimulated to produce and liberate an hormone, known as **secretin.** This is conveyed by the local blood-circulation to the pancreas, causing that organ to liberate pancreatic juice. Thus the flow of this juice occurs only after a meal has been taken, and is not continuous.

A further hormone, **cholecystokinin,** is produced in the walls of the early part of the small intestine. It is conveyed in the blood-stream to the gall-bladder, which it stimulates to contract, thus forcing the bile along the bile-duct.

Hormone of Spleen. An hormone, known as **acetyl choline,** is believed to be produced largely in the spleen, and to have a marked depressor effect on circulation of blood.

Thus these hormones constitute a large part of what may be described as the chemical environment of the organism. It is interesting and important to note their presence in developing embryos, where they are known as organisers. In the frog, for example, they are produced by cells at the dorsal lip of the blastopore, and the removal of this organ stops differentiation. It may well be that the development of different sets of organs is controlled by different organisers. But that the dorsal lip of the blastopore has other developmental significance besides that of producing organisers is shown by the fact that the grafting on of an extra dorsal lip at the gastrula stage may result in the formation of two sets of organs.

CHAPTER XXX

ADAPTATION TO ENVIRONMENT

It is an abundantly evident fact that living organisms are so constructed as to function in accordance with the requirements imposed by their environment. So widely occurring is this phenomenon of adaptation to environment that any absence of it is at once regarded as an anomaly. An adaptation may best be defined for biological purposes as a special form of a general structure. Such adaptations are apparent not only in the broader, morphological features of large groups of animals, but may be discerned as detailed, anatomical modifications serving as criteria of distinction between species. A study of the following examples will serve to make clear these characteristics of adaptations. The significance of so-called physiological variations is discussed on page 324.

Adaptations amongst Vertebrata. One of the most obvious features of the anatomy of vertebrates is their possession of two pairs of pentadactyl limbs. These constitute the "general" structure, referred to in the above definition. But in the different classes of vertebrates this primitive limb becomes variously modified. Thus in the fish it assumes the form of a flattened fin to aid in progression in water. Though in modern forms it is far from pentadactyl it is undoubtedly homologous with—i.e. of the same evolutionary origin as—the limb of the Tetrapod. In birds, bats and pterodactyls the fore-limbs become modified, though differently in each case, to accommodate flight, whilst in the remaining tetrapods they are ambulatory in function. Finally, in the Anthropoids, the digits become prehensile. But much more detailed specialisation has occurred, as well as these broad modifications of the primitive plan. Thus in the group of mammals known as the Ungulata the limbs have become adapted for rapid locomotion through the elongation of the third (as in the Perissodactyla) or the third and fourth (as in Artiodactyla) digits (see page 271). In burrowing animals the claws come to be directed backwards so as to facilitate digging. The whale, in accordance with its reassumption of an aquatic mode of life, has almost lost its limbs. Thus amongst mammals themselves it is apparent that the general structure has become particularised in form in many groups.

The heat-regulation mechanism in mammals is another instance of adaptation, developed on account of the warm-blooded character of members of this group. Glands are present in the skin of lower forms, but in mammals these become modified to pour on to the surface a thin, watery secretion, which, on rapid evaporation, results in reduction of body-temperature. Likewise, in lower forms, a number of epidermal structures in the form of scales make their appearance. Though hair is almost certainly not a direct development of scales the two are often closely associated and arise in somewhat similar manners. Hair affords the principal mechanism of heat-regulation. Muscles are developed in relation to the skin of all vertebrates. In mammals these can cause shivering, so that body-temperature may be raised. Similarly the skin of all vertebrates is to some extent vascularised, especially in the Amphibia. In mammals the capillaries in the skin may be readily contracted or dilated, so that the amount of blood brought to the surface is decreased or increased respectively. In this way heat may be either conserved within the body or expelled to the exterior.

Lastly, the development of a special respiratory channel may be noticed. In Amphibia air is merely gulped into the mouth, making its entrance partly through the nostrils. The upper jaw is fringed by a pair of maxillæ. But in mammals the development of a separate respiratory channel has been completed, for shelves of bone grow in from the maxillæ to fuse in the middle line, thus constituting the false palate. This is continued behind by a mass of tissue forming the soft palate. This nasal passage opens into the pharyngeal region by the secondary choana. In order to facilitate the passage of food through the pharynx to the œsophagus the glottis (opening of the larynx) must be guarded by an epiglottis. In the whale the glottis may be raised so as to open right into the secondary choana. This individual peculiarity doubtless serves to accommodate respiration while the mouth is full of water.

Examples from Invertebrata. It must be realised that in both this and the preceding paragraph only a few examples are selected from the legion which exists. Those drawn from the invertebrates will be chosen so as to show the adaptive significance of coloration. An insect may become protectively coloured in two contrasted ways. In the first place it may come so perfectly to simulate the colours of its customary environment as to be inconspicuous. In such a case the adaptation is said to take the form of protective resemblance. The most obvious and probably the most perfect examples of insects displaying this type of protective coloration are the stick- and leaf-insects, whilst the green colour of the caterpillar of the hawk-moth is interrupted by black lines, and thus the larva is inconspicuous amongst the foliage on which it lives.

The opposite type of coloration is that whereby an insect, developing gaudy and brilliant hues, warns its potential enemies that it can inflict considerable damage on them. Thus this aggressive type of coloration is common amongst noxious insects. The wasp, hornet and bee afford good examples of members of this group. The mere ability to inflict harm is not sufficient: it must be advertised. But whilst it is advantageous for a noxious insect to advertise its powers of effecting damage, it is equally so for an innocuous species to display similar coloration, for it thereby gains the same respect as the form which it simulates. This phenomenon is known as mimicry, and many examples of it are found amongst the Insecta. Thus clear-wing moths at first sight resemble wasps, though they are actually unable to sting, whilst drone-flies and bees are superficially similar in appearance. One of the best known cases amongst butterflies is that of *Papilio polytes*. The female of this species exists in three forms, the *polytes*, the *cyrus* and the *romulus*. The first-named resembles the male, whilst the other two are similar in coloration to members of a different genus, alleged to be distasteful.

Embryological Adaptations. Structural features often become modified in the embryos of some species, as well as in the adult stages. In the Amniota the embryonic membranes are developed to assist in the nutritive and respiratory processes of the embryo, as well as in the regulation of its environment. In lower forms—e.g. the chick—the allantois serves only for respiration, whilst in mammals it becomes modified to form the placenta, accommodating both respiration and nutrition. In still lower forms—e.g. the frog—the allantois is represented by the urinary bladder, and has no special, embryological significance.

General Relationship between Living Organisms. Any student of biology cannot but be impressed by the high degree of interdependence between living organisms. This is perhaps most markedly so in relation to food supply, and the most important feature lies in the mutual connexion in this respect between animals and plants, considered collectively. Thus plants normally feed on water, carbon dioxide and mineral salts. Of these substances the supply is almost unlimited, for cyclical changes result in their continuous replacement. In the process of photosynthesis, whereby plants, with the aid of chlorophyll and in the presence of sunlight, build up water and carbon dioxide to form sugars, oxygen is evolved to the extent of six molecules for every molecule of sugar synthesised. Thus, in general, plants remove carbon dioxide from the air and replace it by oxygen. But in the process of respiration animals take in oxygen from the air and give out carbon dioxide. This occurs also in plants, but to a very limited extent, for, owing to their attached mode of life, plants require but little energy compared with that demanded by animals. Thus a balance is effected between the gaseous reactions of animals and those of plants, as suggested in the equation—

$$6CO_2 + 6H_2O \rightleftharpoons C_6H_{12}O_6 + 6O_2.$$

In this way it will be seen that animals and plants together maintain constant the gaseous constitution of the atmosphere. Not only so, but also it will become apparent that all animals depend ultimately for their existence on plants. Suppose species of animal *A* preys on species of animal *B*, and this in turn on *C*. This food-chain, as it is called, may be extended to a considerable length by a careful selection of examples, but ultimately it will end with a species of animal which lives on plants. Thus the whole chain of species of animals would perish but for the existence of plants. It is apparent, therefore, that all living organisms are interconnected in a general way through food supply.

Individual Relationships. As well as this general connexion between various groups of animals and between animals and plants as a whole there exists a much more intimate set of relationships between individual organisms. Associations of various types occur between two such individuals, varying in degrees of intimacy. Thus two organisms may become associated to the benefit of one of them and the complete indifference of the other. This state of affairs is known as **commensalism.** On the other hand both members of the partnership may reap some benefit, and here the union is termed **symbiosis.** This may be developed to such a degree that either one or both members of the association may become incapable of existence in the absence of the other. Finally, the association may result in benefit to one party, but may work to the detriment, or even the death, of the other. This condition is known as **parasitism.** Each class will be dealt with briefly in turn.

Commensalism. The dogfish is frequently found to have attached to its ventral surface a small suck-fish (*Echensis*). Attachment is effected by means of the dorsal fin of the suck-fish, for this structure becomes modified to form a sucker. This is, then, an adaptation—a special form of a general structure. The suck-fish is sufficiently small not to inconvenience the dogfish, but the latter, being a voracious feeder, is also a waster. In consequence *Echensis* is liberally supplied with food. There are also instances of commensalism involving more than two organisms in the association.

Thus the hermit-crab, *Eupagurus*, lives in the shell of a whelk, often accompanied by other small Crustacea. On the outer surface of the shell may be borne a sea-anemone. Actually there is some reciprocity of benefit in this association, for the hermit-crab is an active animal and moves rapidly about the ocean, thus carrying the anemone with it, so that this latter is continually being brought to abundance of food. But, owing to its nematocysts, the anemone actually protects *Eupagurus* from attacks by fish, so that this is almost an example of external symbiosis. An example of pure commensalism may be cited in the case of the gad-fly. Gad-fly eggs are frequently swallowed by birds, and commence development within their intestine. These embryos are deposited with fæces of the birds on the teats of the mammary glands of Ungulata, where they obtain copious supplies of food.

Symbiosis. The reciprocity of benefit referred to above is characteristic of symbiosis. The commonest example of this phenomenon is the presence of non-cellular algæ in certain animal cells. These algæ are known as the *Zoochlorellæ* and *Zooxanthellæ*, and they are common in the Cœlenterata, exemplified by *Hydra*. Being of typical plant structure these cells photosynthesise sugars from water and carbon dioxide. The latter constituent is provided as a result of respiration by the animal, whilst the oxygen liberated in photosynthesis assists in the animal's respiratory process. Nitrogen- and phosphorus-containing waste products from the animal are utilised by the plant inclusions, whilst the excess of these elements, over and above what the plants require, is reconveyed to the animal in an assimilable form. In practice, however, a certain degree of independence is retained by either or both symbionts, as shown in the following examples.

Convoluta, a marine genus of free-living flat-worm, exists in two specific forms—*C. paradoxa* and *C. roscoffensis*. Each contains algæ in its constituent cells. *C. roscoffensis* in early life is a voracious feeder, but later loses the power of taking in solid food and eventually ingests its own algal inclusions before dying. *C. paradoxa* knows no such abstemious fits, but feeds holozoically throughout life. Both species at birth are colourless, and so may remain if reared in carefully-filtered water. But these forms never attain maturity, dying apparently of nitrogen- and phosphorus-starvation. The importance of these algal inclusions with regard to metabolism of compounds of nitrogen and phosphorus is further emphasised by the fact that these coloured *Convoluta* possess no excretory organs. Thus *C. roscoffensis* has become too degenerate as a result of symbiosis, and in losing its powers of feeding holozoically it has cast too great a burden on its algal inclusions ; the whole therefore dies. *C. paradoxa* actually retains a considerable degree of independence. The alga of neither species can exist apart from its symbiont *Convoluta*. Infection is normally effected by the inclusion of algæ in the egg-capsules. Since the eggs are laid in conditions of darkness the algal inclusions remain at first colourless, its pigment being developed only on exposure to light.

In the above examples it will be clear that general physiological processes have become specialised, so that the characters exhibited may be regarded as physiological adaptations. Now life-processes must be accommodated by structures possessed by the organism in question. It follows, therefore, that physiological adaptations must be regarded as evidence of the existence of anatomical adaptations. The loss of the power of independent existence by the algal inclusions of *Convoluta* may be due to nuclear degeneration, or merely to the inability to synthesise sufficient protein from the low concentration of nitrogen- and phosphorus-containing salts in sea-water. The species of *Convoluta*, on the other hand, present adaptations in their nutritive and excretory processes.

Parasitism. Several cases of parasitism have already been encountered (Chapters III, V and VI). It will be convenient here to summarise the adaptations to this mode of life displayed by the organisms which resort to it. There is in most cases a general degeneracy of structure, developed in accordance with the extreme restriction of environment. Nutrition is most importantly influenced, for the supply of food is almost unlimited and continuously available. At the same time an endoparasite, living in the alimentary tract of its host, must secrete substances over its general body-surface in order to prevent its being attacked by the digestive juices of its host. But while the conditions under which a parasite lives are ideal the problem of distribution is acute, for it is likely that it may prove fatal to its host. Thus there is often a complicated life-cycle to be passed through before the eggs, laid by one adult parasite, themselves become further adults. There is excessive multiplication to increase the chances of propagation, for many eggs will perish through failure to reach the particular host in which the organism is parasitic. For purposes of distribution there is produced a resting stage, capable of withstanding severe degrees of adversity. Often this stage is taken up by an intermediate host, within which a certain amount of development may occur, but the adult form is not attained until the parasite reaches its true host. Accordingly, the intermediate host is usually the organism largely preyed upon by the true host. The significance of the term " adaptation " is readily understood when it is considered in relation to the structural peculiarities of parasitic organisms.

CHAPTER XXXI

CLASSIFICATION

THE vast assemblage of organisms constituting the animal kingdom must necessarily be arranged in groups, the criterion for such arrangement being morphology. At first the broadest distinguishing features are looked for. Thus it is found that the bodies of some animals are divided up into cells, whilst those of others are not so divided. On this characteristic the Protozoa (non-cellular) are separated from the Metazoa (cellular). Between these two come the sponges (Porifera), whose bodies are composed of semi-independent cells. The Metazoa are themselves capable of further subdivision into two large groups, namely the Diploblastica, characterised by the possession of only two layers to their bodies, namely ectoderm and endoderm, and the Triploblastica, having a layer of mesoderm between the endoderm and ectoderm. Each of these groups is further subdivided into a number of comprehensive collections, known as phyla. The various phyla will be found listed in the classificationary table at the end of this chapter, and a single example will now be selected and considered in detail, so that it may be realised how the remaining groups also are subdivided.

Thus the phylum Chordata contains all the Triploblastica which possess bilaterally symmetrical, segmented bodies, having a closed blood-vascular system, an hollow, dorsal, central nervous system, a spacious cœlom, a notochord and gill-slits. This is further subdivided into two subphyla, namely the Cephalochordata and the Craniata. The former, exemplified by *Amphioxus*, contains forms which have a persistent notochord extending throughout the entire length of the animal, numerous gill-slits, subdivided by tongue-bars, and an atrium, whilst there is no clear differentiation of head, limbs, heart or brain, nor is there a skeleton of cartilage or bone. The subphylum Craniata exhibits markedly contrasted characters. Thus the notochord does not extend to the extremities of the animal, and it is replaced in later life by cartilage or bone. Tongue-bars are absent, whilst the number of gill-slits is small: in some forms they disappear in the adult. As well as an internal skeleton of cartilage or bone there are present a well-developed head, brain, heart and usually two pairs of limbs. Further subdivisions of the subphylum Cephalochordata are beyond the scope of the present book, but the various groups of the Craniata are important. This subphylum is primarily subdivided into two branches, namely the Cyclostomata and the Gnathostomata. The former, exemplified by the lamprey (*Petromyzon*), have circular, suctorial mouths, whilst the mouths of the Gnathostomata are bordered by upper and lower jaws. The branch Cyclostomata is divided into class Cyclostomata (living forms) and class Ostracoderma (extinct forms). The branch Gnathostomata is divided into five classes, namely Pisces (fish), Amphibia, Reptilia, Aves (birds) and Mammalia. Each of these is further subdivided successively into orders, genera and species. Thus the class Pisces consists of two grades—the Chondrichthyes and the Osteichthyes. The former have cartilaginous skeletons and the latter bony. The latter grade is then further subdivided into two subclasses, the Teleostomi and the Dipnoi. All the bony fish except the three constituting the Dipnoi belong to the Teleostomi. The Reptilia, Aves and Mammalia together constitute the grade Amniota, characterised by the formation of an amnion during development. The land-living Gnathostomata—i.e. all the classes except the fish—are usually grouped together as the Tetrapoda. The characters separating each group become less extensive passing from phyla to species. To a considerable degree they must be arbitrary, but, as the modern scheme of classification has been worked out, attempts have been made to ensure that each of the orders, for example, in one class differs from the remaining orders of that class to the same extent as orders of another class differ amongst themselves. Whether or not this has been achieved is a matter of opinion, but one category of classification does rest on precise definition : it is the **species.** Two organisms are said to belong to the same species if, as a result of their interbreeding, there is produced no diminution in fertility. It is not sufficient that two organisms breed and give rise to fertile offspring. This process must be continued through many generations, and it must be proven that fertility is not diminished. This being so the organisms are assigned to the same species.

Nomenclature. An animal is referred to by two Latin names, the first of which is its generic name (i.e. the name of the genus to which it belongs) and the second its specific name (i.e. indicating its species). Thus the frog is known as *Rana temporaria.* The full classificationary position of the frog will be, therefore, species *temporaria*, genus *Rana*, order Anura, class Amphibia, branch Gnathostomata, subphylum Craniata, phylum Chordata, belonging to the Triploblastica, of subkingdom Metazoa and kingdom Animalia.

Significance of Classification. Such a scheme of classification must be taken to express not only the differences between various groups of animals, but the relationships between them. The theory of organic evolution postulates a community of descent for all living organisms. But it must be borne in mind that each group has become very specialised within itself, so that points of comparison between one group and another are not always readily apparent. When members of one group became modified to give rise to a new group it was the simple and primitive forms alone which could undergo this change. Assuming this process to have occurred in this way it is obvious that identical structures will be represented in different groups of animals, though they may be superficially dissimilar. But by tracing the development of the structures in question it is often possible to elucidate their significance. Examples of this phenomenon have already been referred to. Thus the endostyle of *Amphioxus* develops in precisely the same manner, up to a point, as the thyroid gland of members of the Craniata. The two structures are therefore said to be **homologous.** Two structures are homologous when they have the same developmental history. But the theory of evolution implies that the later one—e.g. the thyroid gland of Craniata—has been formed by modification of the earlier one—e.g. the endostyle of forms allied to *Amphioxus.* Thus homologous structures have not only the same individual, developmental history, but also the same evolutionary origin. This is, perhaps, the more satisfactory definition of homologous structures. There are innumerable examples of this phenomenon to be drawn from the Chordata. Thus the wheel-organ and tongue-bars of *Amphioxus* are respectively homologous with the hypophysis and thymus gland of Craniata, whilst homology between various parts of the members of the different classes of the Craniata is at once apparent. Thus the liver, for example, is homologous in all five classes of the Gnathostomata. In this connexion the student is advised to consult Chapters XXI and XXII with a view to tracing homologies between parts of the vascular and excretory systems throughout the Craniata.

Somewhat akin to homology another phenomenon may be mentioned. It is possible that two structures in comparatively unrelated forms may serve the same purpose and yet not be homologous—i.e. not of the same evolutionary descent. Such structures are said to be **analogous.** By contrasting vertebrates and invertebrates numerous examples of this phenomenon may be discovered. Thus the wings of insects and birds are analogous structures, as are the mouth parts of insects and the jaws of the Gnathostomata. The student will be able to discover an almost unlimited number of examples for himself along the same lines.

High and Low Types of Organism. At the one end of the scale of classification occur the Protozoa. These are regarded as the lowliest of animals on account of the fact that they are forced to carry out all their life-processes with only a minute portion of non-cellular protoplasm comprising each of their bodies. This fragment is, therefore, completely unspecialised, and *Amœba* affords a good example of such an organism. Nutrition, respiration, locomotion, conduction of stimuli, excretion and reproduction involve the whole organism. Every portion of it may take part in every process. But in all forms above the Protozoa the body is divided into cells, the various cells becoming specialised to perform certain functions to the exclusion of others, and thus becoming mutually interdependent. The higher up the classificationary tree we proceed the nearer to perfect does this specialisation become, culminating in mammals, and particularly in man. The parts of this higher type of organism have lost their powers of independent existence, so that the organism as a whole, and not each component part of it, possesses individuality.

But the terms "high" and "low" amongst animals may be interpreted in another manner, for in a given group—say a phylum—some members may be described as low or primitive, whilst others are high or specialised. A reference to insects will make this clear. A cockroach is a low or primitive insect because it exhibits all the typical insect characters in the simplest possible form. Thus it is clearly segmented throughout, its mouth parts are unmodified and its life-history unspecialised. But in *Aphis*, for example, segmentation is obscure in the abdomen, the mouth parts are adapted for the sucking of plant juices, whilst the life-history is very much complicated in adaptation to seasonal conditions. In this sense the *Aphis* is a specialised or "high" type of insect. Thus, as evolution proceeds, the differences between one group and another become progressively more pronounced, for specialisation occurs within each group, resulting in their structure becoming more and more divergent.

Thus in studying the following scheme of classification it must be borne in mind that not only do the members of one group differ from those of another, but also the members of quite large groups have many characters in common. A frequent error in the study of classification is to note the differences but pass over the similarities between various groups. The diagnostic features of each large group will be found in the chapters concerned with the types drawn from them.

Subkingdom	**Protozoa**
PHYLUM	PROTOZOA
Class	Flagellata (Mastigophora)
"	Rhizopoda (Sarcodina)
"	Ciliata (Infusoria)
"	Sporozoa
Subkingdom	**Metazoa**
PHYLUM	PORIFERA
Group	Diploblastica
PHYLUM	CŒLENTERATA
Class	Hydrozoa
"	Anthozoa
"	Scyphozoa
Group	Triploblastica
PHYLUM	PLATYHELMINTHES
Class	Turbellaria
"	Tramatoda
"	Cestoda
PHYLUM	ANNELIDA
Class	Polychætæ
"	Oligochætæ
"	Hirudinea
"	Archiannelida
"	Echiuroidea
"	Myzostomaria
PHYLUM	ARTHROPODA
Class	Insecta
"	Crustacea
"	Arachnida
"	Myriapoda
PHYLUM	MOLLUSCA
Class	Lamellibranchiata
"	Gastropoda
"	Cephalopoda
PHYLUM	ECHINODERMA
PHYLUM	CHORDATA
Subphylum	Cephalochordata
Subphylum	Craniata
Branch	Cyclostomata
Class	Cyclostomata
"	Ostracoderma
Branch	Gnathostomata
Class	Pisces
Grade	Chondrichthyes
"	Osteichthyes
Class	Amphibia
"	Reptilia
"	Aves
..	Mammalia

CHAPTER XXXII

PRACTICAL WORK

AMŒBA

LIVING specimens may be obtained from the mud at the bottom of fresh-water ponds, whilst others occur in the soil. The latter may be obtained in the following way. A little hay is chopped up and introduced into a flask containing about 500 c.c. of water. The whole is then heated on a boiling water-bath for about an hour. The resultant solution is filtered and made just alkaline with two drops of sodium hydroxide solution. The liquid is then thoroughly boiled to effect sterilisation. It is then divided into two lots, and into each is introduced about half a gramme of garden soil. After a few days *Amœba* should be present in the culture fluid.

These are examined alive in order to discover the method of locomotion.

Killing, Staining and Mounting. Since the animal is so small all these operations must be carried out on a microscope slide. The *Amœba* is mounted in a drop of water and covered with a cover-slip. A drop of Bouin or osmic acid is then placed at one edge of the cover-slip and drawn through by means of a piece of blotting paper inserted just beneath the cover-slip at the opposite edge. The slide must be examined at frequent intervals throughout the whole preparation so as to ensure that the organism has not been drawn through with the various fluids. It is a good plan to put each successive fluid to be drawn through at the edge opposite to that at which the previous one was introduced. If Bouin has been used 70% alcohol is next drawn through : if osmic acid, water is used. Iron alum solution is now drawn in and left thus for one hour. This is then removed by drawing through several lots of water. Iron hæmatoxylin is now drawn in, and again the slide is left for one hour. The purpose of the iron alum is to act as a mordant, and after subjection to iron hæmatoxylin the whole animal becomes black. Iron alum is then reintroduced and the slide examined at intervals until only the nuclei are black. This process of dissolving superfluous stain is known as **differentiation.** When only the nuclei are black water is run in to remove the iron alum. 30%, 50%, 70% and 90% alcohols are drawn through successively, and finally two lots of absolute alcohol. Next xylol or clove oil is drawn through in two successive lots, and finally the cover-slip is raised so that a drop of Canada balsam may be spread over the organism. The cover-slip is replaced and a permanent preparation is thus completed.

EUGLENA

This is found normally in small, green ponds, and may be treated similarly to *Amœba.*

PARAMECIUM

A culture of *Paramecium* may readily be made by the addition of hay to a specimen of muddy water obtained from a pond known to contain *Paramecium.* It may be stained in the manner already described for *Amœba.*

MONOCYSTIS

Both species of *Monocystis,* together with the various stages of its life-cycle, may usually be obtained by teasing out on a slide with a pair of needles the vesiculæ seminales of a large earthworm. Once thus identified they may be stained in the manner described for *Amœba.*

HYDRA AND OBELIA

Hydra is abundant in ponds, ditches and slow-running streams. It is visible to the naked eye, and therefore staining operations may be carried out in a watch-glass. If preferred they may be effected on a slide, the fluids being introduced and removed by means of a fine-pointed pipette. The organism is fixed—i.e. killed and rendered stable in chemical form—in mercuric acetic (see page 339) for half an hour. It is then washed in 70% alcohol containing an excess of iodine. Then borax carmine is introduced, and the preparation is left in the stain for about an hour. The stain is then replaced by 70% alcohol and the preparation examined. If over-stained it is left thus for a while and some of the stain is dissolved out. The 70% alcohol is then replaced, first by 90% and then by two successive lots of absolute alcohol, allowing some five minutes in each. Finally xylol is introduced. The preparation is then transferred by means of the fine pipette to the slide (unless all the operations have been carried out on the slide), and mounted in Canada balsam.

Obelia is found commonly attached to the fronds of sea-weed, and permanent preparations of it may be made as for *Hydra.*

DISTOMUM AND TÆNIA

These may best be studied by means of ready-made slides. The actual specimens themselves should be examined if possible with a view to determining their external features.

LUMBRICUS

The animal should be examined in the living condition, and its various external features observed. It can then be killed by subjection to chloroform vapour and dissected according to the instructions found in practical books of zoology. Since earthworms are readily available it is possible to concentrate on one system in a given worm, taking fresh specimens for each new system. The dissection of the nervous system is facilitated by the immersion of the specimen after opening in a 4% solution of formaldehyde for a day or more, since this hardens nervous tissue.

The preparation of a transverse section of an earthworm may well be undertaken. This process is important, since the same technique is equally applicable to the preparation of sections of other whole, or parts of, animals. The worm thus to be used is retained in moist sawdust for a day or so in order that food may be thoroughly evacuated. It is then fixed in mercuric acetic for about half an hour, being cut into short portions (about half an inch) once it is dead. The fixative is then washed out with 70% alcohol containing an excess of iodine. A few portions are then placed successively in 90% and two lots of absolute alcohol for about ten minutes each. Following this they are placed in two lots of xylol for about fifteen minutes each. Into the pot containing the portions of the earthworm and the xylol paraffin wax (m.p. about 50° C.) is flaked, and the whole is left on top of a thermostat (interior temperature about 60° C.) for half an hour. Next the portions are placed in a pot containing molten wax in the thermostat for half an hour. A small mould—anything in the nature of a deep metal or glass ring will do—is then greased and filled with molten wax. Each portion of the worm is placed in the molten wax in such a mould, and the surface of the wax is cooled by being blown upon. As soon as a film is formed over the surface of the wax the whole is immersed in cold water for ten minutes. The disc of wax, with the specimen embedded in it, is then removed from the mould, and cut with a sharp scalpel into a rectangular block, the specimen lying parallel to four of the faces of the block. Sections are then cut by means of a microtome. For all ordinary purposes the Cambridge " Rocking " type of microtome is perfectly satisfactory, costing rather less than £7, inclusive of all accessories. A microscope slide is now smeared with a solution formed by adding one drop of Mayer's albumen (page 339) to 10 c.c. of water. A single section is now placed on the smeared part of the slide and carefully dried over a very low Bunsen or spirit-lamp flame. The slide is then immersed in a grooved Coplin jar containing xylol. This dissolves the wax, but if properly cemented on the section will not leave the slide. The slide is then transferred successively to similar vessels containing absolute (two lots), 90%, 70%, 50% and 30% alcohol, remaining for five minutes in each, and finally it is placed in water. To ensure the complete removal of alcohol it is placed in a second lot of water, and then for half an hour in a grooved Coplin jar containing borax carmine. This stains both nuclei and cytoplasm red, so it is differentiated (page 330) until the cytoplasm is colourless by being placed in alcohol acidified with hydrochloric acid. When this stage is reached, as discovered by examination under the microscope at frequent intervals, the slide is rinsed in water and then placed for half an hour in picro-indigo-carmine. At the end of this time it is rinsed in acid alcohol and examined. If the section appears too blue it is differentiated in tap water, and if too yellow in 70% alcohol. When a satisfactory balance has been obtained the slide is taken up through the alcohols and finally placed in two lots of absolute for some five minutes each. From here it is transferred to two successive lots of xylol, and then a drop of Canada balsam is spread over the section and a cover-slip lowered into position. The nuclei, stained by the borax carmine, will be red, the connective tissue blue with indigo-carmine, the epithelia and muscles yellow with the picric acid, whilst the other tissues will be various shades of green, having taken on some of the yellow and the blue stains.

An ovary and a nephridium should each be removed, stained and mounted. The staining technique for either structure may be that employed for *Hydra*. In order to make fairly certain of including the nephrostome, part of the septum which the nephridium pierces should be removed along with the nephridium itself.

PERIPLANETA

The external characters should first be thoroughly mastered, and detailed instructions for dissection will be found in a practical text-book. For this purpose the animal is best fixed in position by being placed in molten wax with the dorsal surface protruding. Care must be taken that the upper surface of the head is also above the level of the wax, since it will have to be opened in order to dissect out the cerebral ganglia.

Three additional preparations should be made in conclusion.

These are the tracheal tube, salivary glands and mouth parts. The first two should be removed and stained in precisely the same manner as described for *Hydra*, and then mounted in Canada balsam. In order to prepare the mouth parts for examination the head should be cut off at the neck, and boiled for some minutes in sodium hydroxide solution. Each mouth part may then be removed from the head and placed in a dish of water. It is important that each part to be removed be clasped firmly *at its base*, so as to ensure its coming away whole. Stout forceps are found best for holding the head itself during these operations, and fine ones for the removal of the mouth parts. The head must be gripped from the back so as not to injure the remaining mouth parts whilst the first ones are being removed. Being hard structures they may be transferred from water to 70% alcohol for ten minutes, and then straight to two lots of absolute for ten minutes each. They are then placed in xylol, and afterwards mounted in the usual way. It is important in arranging them in the Canada balsam to place them close together in correct, relative orientation. When the cover-slip is lowered on to them they move a convenient distance apart.

Other Insects

The external features of various insects themselves and of stages in their life-histories should be examined, and certain preparations may conveniently be made, such as the mouth parts of the bee and butterfly.

Astacus

The external features are of tremendous importance, and the appendages of one side should be carefully removed, retained in order and drawn. The smaller ones may require certain magnification.

The nervous system is the most important dissection for present purposes, and other organs should be noted in passing.

If time permits a longitudinal section of the eye may be cut by embedding the organ in wax in the manner already described (page 332).

Anodonta and Helix

Examination of external features and subsequent dissection are the chief tasks. The radula of the snail may be extracted and prepared. The buccal mass is removed and some of the soft tissue surrounding the radula cut away. The radula is then boiled in sodium hydroxide solution, and when the remaining tissue has fallen away from it it is washed in water. It is then placed successively into 70% and two lots of absolute alcohol, then into xylol, and finally mounted in Canada balsam.

ASTERIAS

External features must first be examined. Brief instructions as to dissection will be given here, since they are omitted from many practical books. Cut round the margin of the animal, so that the cut separates the oral and aboral surfaces. Then cut through the structures holding the two halves together, namely œsophagus, muscles and stone canal. In the oral half look for the stone canal, axial sinus and axial organ, nerve-ring, water-vascular ring and Tiedemann's bodies : in the aboral half note the stomach, pyloric cæca and reproductive organs.

Finally a transverse section of the arm should be examined.

AMPHIOXUS

External features should be examined, but the organism is too small to allow of satisfactory dissection. Most importantly transverse sections through different regions of the animal must be examined, and if time permits they should be prepared and stained by the student in the manner described for sections of the earthworm (page 333).

SCYLLIUM

As well as the usual examination of external features and dissection the skeleton must be studied. This may be prepared by keeping the animal in 70% alcohol for some days, and then immersing it for a few moments in almost boiling water. The soft parts can then be removed, and the skeleton thus obtained is best kept in dilute alcohol (20%).

RANA AND LEPUS

These animals must be dealt with very thoroughly, and should be dissected at least three times each. The skeleton is an important feature. As well as studying an articulated skeleton to get clear the relative positions of the bones, the individual bones should be examined. The bones should be cleared as far as possible of flesh and then put into cold water for some weeks. They must then be thoroughly washed and exposed to the sunlight for two weeks or so for bleaching, being repeatedly dipped into water and allowed to dry. Boiling often results, in the case of the limb bones, of the head coming away from the shaft, thus rendering them useless.

Preparations of various tissues must be made and examined. A piece of muscle should be teased out on a slide and stained with borax carmine, as described for *Hydra*.

Preparation of blood is important. Two slides are thoroughly cleaned in acid alcohol, and at one end of one of them a small drop of blood is placed. The other slide is then drawn across it, being held at an angle of about 45°. It is pressed hard on to the slide bearing the blood, so that a very thin smear is formed. The slide is now dried. A few drops of Leishmann's stain are now spread over the slide so as to cover the blood-smear, and the whole left for one minute. Double the number of drops of water are now added to the stain on the slide, and these are spread about to form an even mixture. After fifteen minutes the slide is washed in distilled water, and dried with blotting paper. The blood can now be examined under oil immersion without use of balsam and a cover-slip. The erythrocytes appear pink, whilst the nuclei of the leucocytes will be blue-purple. Parasites in the blood will have their cytoplasm stained blue and their nuclei red.

Alternatively methylene-blue-eosin (Giemsa) may be used. The smear is made as before and, after drying, the slide is put into absolute alcohol for five minutes. The stain is prepared by adding one drop of the stock Giemsa solution to every c.c. of distilled water. Enough stain to fill a clock-glass is made thus, and the slide is placed in it for from ten to thirty minutes. It is then washed in distilled water and dried by blotting. Erythrocytes will now be mauve, parasites blue and leucocytes reddish-violet.

Other tissues must be embedded in wax and sectioned prior to staining. Suggested tissues for this purpose are liver, pancreas, kidney, testis and lung. The process of embedding has already been described (page 332), but in the present case Ehrlich's hæmatoxylin and eosin are suitable stains. Starting from the stage where the slide has cemented on to it a section of the tissue to be examined, the slide is now put into xylol to remove the wax. It is then transferred to absolute alcohol and brought down through progressively decreasing strengths of alcohol to water. It is next put into Ehrlich's hæmatoxylin for about fifteen minutes, and subsequently differentiated in acid alcohol until only the nuclei are blue. Differentiation is stopped by returning to water. It is now placed in eosin for three minutes, and then brought up quickly through the alcohols, allowing about one minute in each of the non-absolute mixtures and two minutes in each lot of absolute. It is transferred to xylol, with two minutes in each of two successive lots, and finally mounted in balsam. This is a useful technique for general tissue staining, since the nuclei are coloured blue and the cytoplasm red.

EMBRYOLOGY

Prepared slides showing the various stages of development of *Amphioxus*, *Rana* and *Gallus* should be studied. Except in the case of *Rana* it is unlikely that any further practical work may be undertaken, for conditions of development cannot readily be reproduced in the case of the other two types unless the student is sufficiently fortunate to have an incubator at his disposal. In that case blastoderms of hen's eggs may be removed and mounted at known intervals. This operation should be done in salt solution, and a watch-glass is dipped into the solution, bringing away with it, on withdrawal, the blastoderm and some solution. The vitelline membrane is released from its attachment to the margin of the blastoderm by means of a needle, and after this the blastoderm is floated on to a slide, on which all further operations are performed. Great care must be taken to keep the blastoderm flat. The salt solution is drawn off the slide and corrosive sublimate is introduced in its place. This fixes the blastoderm in half an hour. The fixative is then washed off and dilute eosin is added for staining purposes. When sufficiently stained the blastoderm is washed, and 30%, 50%, 70%, 90% and absolute alcohols are placed successively on to it. After two lots of absolute alcohol xylol is added, and finally the blastoderm is mounted in balsam.

With *Rana* the problem of tracing development is easier, for spawn may be kept in the laboratory aquarium and examined at regular intervals, so that external features may be watched throughout. If possible transverse and longitudinal sections of embryos at various stages may be cut.

NUTRITION

The chemical tests for various constituents of the food, as detailed in the course of Chapter XXV, should be performed practically.

RECORDS OF PRACTICAL WORK

In the non-biological sciences the student gets accustomed to writing descriptions of qualitative experiments, and calculating results as well in the case of quantitative experiments. But of the greater part of his practical work the zoologist has no such record, for it mostly takes the form of dissection. It is therefore essential that all dissections be well drawn and clearly labelled. It is not enough merely to represent a dissection by a rough diagram, any more than scrappy notes will suffice for a description of a chemical experiment. As far as possible the drawings should be reproductions of the actual dissection, with at most only slight approximation to diagrammatic form. The author hopes that a careful consideration of some of the diagrams in this book, and especially of those reproduced from the "Atlas of Practical Elementary Zootomy," by G. B. Howes, will inspire the student with a sense of pride in his practical note-book. Suggestions may be taken with advantage from text-book figures as to the best way of arranging the organs of a particular system, but the student should make his drawings direct from his own dissections. All drawings should be made with a sharp-pointed pencil, and tinting of the various organs may prove a useful means of attaining clarity. They should not, however, be heavily coloured. A few of the conventions of colouring should be followed, namely arteries in red, veins in blue, and the gut and its diverticula (i.e. endodermal structures) in green. Large organs, such as the liver, should be tinted extremely lightly, especially away from the outline. Cavities may be most conveniently represented by box-shading. A final point worth attention is that all the drawings of a given animal should be grouped together. For this reason loose-leaf drawing books are best, for not only does it render this task easier, but also it means that a subsequent drawing of a dissection previously recorded may be readily substituted for the earlier, inferior one.

Chemical tests on classes of foods are most conveniently summarised in tabular form.

The present chapter is not intended to serve as a complete practical book. It offers suggestions for practical work, and it is hoped that the details of techniques for staining and sectioning will be of service. Detailed instructions for dissection will be found in the laboratory manual, Marshall and Hurst's "Practical Zoology" being highly recommended.

APPENDIX

As well as the ordinary reagents, such as chloroform and various strengths of alcohol, the following are also necessary for the carrying out of chemical tests and staining processes described in Chapters XXV and XXXII.

Where the method of preparation is not indicated it is suggested that they be obtained ready-made.

Fixatives

Bouin.

Corrosive sublimate. Dissolve about 70 gms. of mercuric chloride in 1 litre of water.

Mercuric-acetic. Add 1 vol. of glacial acetic acid to 9 of corrosive sublimate solution.

Osmic acid.

Stains

Borax carmine.

Ehrlich's hæmatoxylin.

Eosin.

Iron hæmatoxylin.

Leishmann's stain.

Methylene-blue-eosin. (Giemsa stain.)

Picro-indigo-carmine.

Other Reagents

α-naphthol.

Benedict's solution (page 286).

Iron alum.

Methylene blue.

Olive oil.

Thymol.

Wax (m.p. 50° C.).

Xylol.

Cement for Fixing Sections

Mayer's albumen. Mix equal volumes of fresh egg albumen and glycerine. For use add one drop of this stock solution to 10 c.c. of distilled water.

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